CENTRE FOR EVIDENCE-BASED CONSERVATION

SYSTEMATIC REVIEW NO. 17:
ARE CURRENT MANAGEMENT RECOMMENDATIONS FOR CONSERVING SAPROXYLIC INVERTEBRATES EFFECTIVE?

REVIEW REPORT
(FINAL REPORT)

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SYSTEMATIC REVIEW SUMMARY

Background

Throughout Europe, saproxylic insects have been identified as a highly threatened community of invertebrates. Conservation management recommendations for saproxylic invertebrates advocate the continuous provision of dead and decaying wood microhabitats that they require for survival. In addition to protecting veteran trees, this can be achieved by leaving fallen dead and decaying wood *in situ* on sites, providing supplementary coarse woody material (CWM), inducing decay in mature trees and strategic planting in order to maintain a balanced age structure of trees in both space and time. Such site-based management interventions may be of importance when used as a conservation tool to bridge gaps between dead wood generations.

Objectives

The primary objective was to systematically collate and synthesise published and unpublished evidence in order to address the question "Are current management recommendations for conserving saproxylic invertebrates effective?". The systematic review aimed to examine whether site-based manipulation of biotic and abiotic factors, such as the provision of supplementary CWM, inducing decay in younger trees or altering the degree of sun-exposure within a stand of trees, can benefit the saproxylic fauna. It was anticipated that the review would draw attention to areas where primary research, or long-term monitoring, would be valuable in order to substantiate the current management guidelines and to initiate evidence-based best practice in saproxylic conservation.

Search Strategy

Relevant studies were identified through computerised searches of the following electronic databases: ISI Web of Knowledge (including ISI Web of Science and ISI Proceedings), JSTOR, Science Direct, Directory of Open Access Journals (DOAJ), Copac, Scirus, Scopus, Index to Theses Online, Digital Dissertations Online, Agricola, CAB Abstracts, English Nature's "WildLink" and the Countryside Council for Wales (CCW) library. Web searches were conducted using the internet meta-search engines Alltheweb and Google Scholar, in addition to inspecting the following statutory organisation websites: UK Department for Environment, Farming and Rural Affairs (Defra), Northern Ireland Department of Agriculture and Rural Development (DARD) and European Union portal (Europa). The specialist publication "Coleopterist" was searched by hand for any appropriate information. No specific non-English language searches were conducted. Bibliographies of traditional literature reviews and articles accepted into the systematic review at the full text stage were examined for studies that had not yet been identified by any other means.

Study Selection Criteria

The criteria, which studies had to meet for inclusion into the final stage of the systematic review, were:

1. *Subject*: any saproxylic invertebrate population or assemblage.
2. *Intervention*: any site-based management action.
3. *Outcome*: desired primary outcomes were change in population density for a target species or change in species richness within assemblages. Nonetheless, studies were not rejected on the basis of outcome.
4. *Type of study*: any.

Data Collection and Data Analysis

Study inclusion assessments were performed and the observed agreement between the two independent reviewers was deemed to be "substantially good". Due to a lack of high quality data (i.e., long-term fully replicated and controlled field-based experiments or investigations) on changes in the long-term persistence of populations, or in species richness within assemblages, no meta-analysis was undertaken. In addition, the variation in type of investigation and range of outcome measures adopted in the studies precluded the use of formal statistical techniques.

Main Results

The available evidence is insufficient to critically appraise the effectiveness of any site-based conservation interventions for saproxylic species or communities in the long-term. However, there is a range of studies describing changes in the saproxylic fauna in response to a variety of habitat management interventions, observed over relatively short periods of time. The research suggests that incorporating a variety of different management actions, such as the retention of dead and decaying wood or the provision of supplementary CWM, into site management plans will increase microhabitat heterogeneity and therefore the diversity of species present on a site.

Conclusions

In the absence of robust, high quality evidence, recommendations relating to the use of specific site-based management interventions would be speculative. However, it is acknowledged that general proposals for the maintenance of suitable microhabitats, such as the protection of veteran trees within the landscape, are based on sound ecological principles and should not be discouraged even though experimentally rigorous evidence is lacking. Further primary research (including long-term monitoring) is required to fill the gaps in our ecological knowledge that potentially weaken the case for the effectiveness of current saproxylic invertebrate conservation action.

The evidence that is available suggests that management priorities should be to improve the diversity, quantity and continuity of dead and decaying wood on sites. Optimising microhabitat heterogeneity by artificially manipulating the orientation and type of CWM on a site may increase number of saproxylic species present and help to buffer populations against environmental change. Conducting such interventions within an experimental framework, and subsequently monitoring the saproxylic fauna throughout the lifetime of the dead wood, will generate important information on the relative value of different CWM constructions for target species/assemblages at each progressive stage of decay. Detailed information on the distribution and autecology of species, particularly those of conservation concern, must continue to be collated and disseminated in order to allow practitioners to allocate conservation resources effectively.

BACKGROUND

1.1 Saproxylic Invertebrates

Speight (1989) defined saproxylic invertebrates as species which are dependent on dead wood during some stage of their lifecycle. In recent years, however, this definition has been developed and refined. Fowles et al. (1999) describe saproxylic species as obligate on microhabitats associated with the processes of decay and damage in the bark and wood of trees, large woody scrub and climbers. The saproxylic fauna is responsible for the mechanical breakdown of woody material (Cavalli & Mason 2003) both directly, by tunnelling and feeding in living trees that are decaying, snags (standing dead trees) and logs (fallen trees, portions of trunks and large branches), or indirectly, through symbiotic relationships with fungi and other micro-organisms that humify wood (Speight 1989). They may, therefore, be broadly classified as either "primary saproxylic consumers" that can actively colonise dead wood, or "secondary saproxylic consumers" that can only exploit dead wood microhabitats once they have been rendered suitable by the action of the primary colonisers (Cavalli & Mason 2003; Cheesman & Wilde 2003).

Fungal colonisation is the preliminary stage in the decay of wood, transforming the tissues of a tree or coarse woody material (CWM) into viable decomposing material suitable for saproxylic invertebrates to utilise. In turn, these invertebrates continue the slow breakdown of the wood, creating a range of specialised microhabitats that mature and differentiate (Hammond et al. 2004). The physical and chemical stability of wood is determined by a cellulose-lignin complex that is particularly difficult to degrade, which ensures that these microhabitats persist over time. However, different types of wood decompose at different rates. For instance, the rate of decay for logs lying on the forest floor is much faster than for standing snags, as the fungal action is accelerated by the moisture content of the soil (Fager 1968; Cavalli & Mason 2003).

Decaying wood and saproxylic invertebrates have a number of key roles to play in terrestrial ecosystems, including capturing carbon, improving the hydro-geological efficiency of the landscape, contributing to biodiversity and perpetuating the formation of humus which increases overall productivity (Cavalli & Mason 2003). The presence of dead wood and saproxylic species, particularly beetles (Coleoptera), in forests, woodlands, parklands or open pasture-woodland indicate that it is high quality mature habitat (Alexander 2004). Indeed, beetles are the most studied and speciose taxonomic group of saproxylic invertebrates (Kaila et al. 1997; Dajoz 2000; Cheesman & Wilde 2003; Alexander 2004).

1.2 Changes in Tree Management & Saproxylic Invertebrate Decline

Throughout Europe, saproxylic insects have been identified as the most threatened community of invertebrates (Berg et al. 1994; Read 2000; Alexander 2004). For example, 50% of the German saproxylic beetle fauna is considered to be endangered (Geiser 1998) and 196 saproxylic insect species are categorised as threatened in Finland alone (Rassi et al. 1992). This is a consequence of a shift towards intensive commercial forestry and agricultural management practices over the last two centuries (Speight 1989), which has dramatically modified the biotic and abiotic processes occurring within forest and woodland ecosystems.

The principal reason for the decline in the saproxylic invertebrate fauna is the removal and reduction in quality of dead and decaying wood within the landscape (McGee et al. 1999; Hale et al. 1999; Fridman & Walheim 2000; Grove 2001; Larsson & Danell 2001; Siitonen 2001). For example, in commercial forestry, dead and decaying wood are frequently cleared from sites to make way for new tree planting, while sanitation felling and burning are employed to protect crops from pest infestation (Winter 1993). Consequently, the number of threatened saproxylic species is particularly high in all countries which have exploited silviculture and harvesting practices and converted deciduous forests into uniform native and non-native coniferous stands (Heliövaara & Väisänen 1984; Mikkola 1991; Warren & Key 1991; Wilson 1992; Väisänen et al. 1993; Haila et al. 1994; Kaila et al. 1994; Siitonen & Martikainen 1994; Kouki et al. 2001). One such region in Europe is Fennoscandia, where the forestry industry is directly threatening the survival of 35% of the saproxylic species (Rassi et al. 1992).

In Britain, the rarest and most threatened saproxylic invertebrates are concentrated in historic parklands and open pasture-woodland (where livestock are grazed in areas with trees present; Rackham 1986). The majority of the endangered fauna are specialists associated with the later stages of wood decomposition and, in particular, the decay of veteran trees (Rose 1976; Harding & Rose 1986; Stubbs & Falk 1987; Speight 1989; Alexander 1996; Alexander 2004). Unfortunately, these trees have been selectively removed from sites where they occurred historically, and are susceptible to damage where they do remain (Bailey et al. 1992; Dobson & Crawley 1994; Nilsson 1997; Kirby & Watkins 1998; Read 2000). A strong positive correlation has been demonstrated between tree age and high saproxylic species-richness (Rose 1976; Harding & Rose 1986; Rackham 1986; Speight 1989; Harding & Alexander 1994), so the preservation and continuity of veteran trees has become a high conservation priority in recent years (Speight 1989; Harding & Alexander 1993; Harding & Alexander 1994; Nilsson & Baranowski 1994; Fowles et al. 1999).

1.3 Saproxylic Invertebrate Conservation

The decline in saproxylic species diversity throughout Europe has only been widely acknowledged in the last few decades (Esseen et al. 1992; Esseen et al. 1997; Alexander 1998). In 1988, the Council of Europe adopted a recommendation on the protection of saproxylic invertebrates and their biotopes (Speight 1989). Prior to this, the majority of species that had been studied were pests of economic interest to commercial forestry (Paviour-Smith & Elbourn 1993; Cheesman & Wilde 2003). Since the 1990s, there has been an increasing recognition of the value of dead wood and the protection of decaying wood habitat is now cited as an environmental concern in forestry policy and procedures in many European countries (Butler et al. 2002).

Detailed knowledge of saproxylic species autecology is relatively limited due to the complexity of the habitat requirements at different stages within their life cycles and the difficulty of detecting species that may be present at low density (Speight 1989; Cheesman & Wilde 2003; K.N.A. Alexander personal communication). However, a high proportion of the saproxylic species of conservation concern are associated with veteran trees and, in Britain for example, ecological groups including the Ancient Tree Forum (ATF) and the Veteran Tree Initiative (VTI) have done much to endorse the conservation of such trees. In turn, this has promoted the maintenance and provision of suitable habitat for the saproxylic invertebrate fauna (Read 2000; Alexander 2004).

Conservation management recommendations for saproxylic invertebrates advocate the continuous provision of dead and decaying wood (refer to Appendix One for a list of publications). In addition to protecting veteran trees, this can be achieved by leaving dead or decaying wood *in situ* on sites, providing supplementary coarse woody material (CWM), inducing decay in mature trees and strategic planting in order to maintain a balanced age structure of trees in both space and time. Most saproxylic invertebrates are specialists and it is unlikely that many trees will satisfy their niche requirements, even on sites with a relatively substantial veteran tree population (Read 2000). Retaining the tree species composition is therefore considered to be of vital importance to the long-term stability and persistence of the local saproxylic fauna (Fry & Lonsdale 1991).

1.4 Review Rationale

A systematic review of all available empirical evidence was proposed by The National Trust (a substantial private charity that owns and manages land throughout England, Wales and Northern Ireland for conservation objectives) in order to evaluate the effectiveness of current site-based management recommendations in regard to conserving saproxylic invertebrates. It was anticipated that the review would draw attention to areas where primary research, or long-term monitoring, would be valuable in order to substantiate the current management guidelines and to initiate evidence-based best practice in saproxylic conservation.

2. OBJECTIVES

2.1 Primary Objective

To systematically collate and synthesise published and unpublished evidence in order to address the following question:

> "Are current management recommendations for conserving saproxylic invertebrates effective?"

2.2 Secondary Objective

To investigate whether biotic and abiotic factors, such as those listed below, can be manipulated through site-based management in order to benefit the saproxylic fauna:

- Provision of supplementary dead and decaying wood (e.g., logs and snags of various construction).
- Provision of simulated dead and decaying wood (i.e., artificially created substrates that mimic logs).
- Promotion of decay and cavities in younger trees.
- The microclimate surrounding dead and decaying wood (e.g., altering the degree of sun-exposure).

3. METHODS

3.1 Question Formulation

The National Trust identified the need for a systematic review to evaluate the effectiveness of current management interventions in regard to conserving saproxylic invertebrates. The specific nature of the question to be addressed was formulated via iterative discussion between UK-based stakeholder organisations with an interest in the result of the review. In total, seven other stakeholder organisations (UK Biological Records Centre, Buglife, Countryside Council for Wales, English Nature, UK Joint Nature Conservation Committee, Royal Society for the Protection of Birds, Scottish Natural Heritage) were contacted and invited to comment on a draft of the proposed methodological protocol, prior to finalisation and initiating the research.

The question is composed of three key elements:

1. *Subject (i.e., the unit of study to which the intervention is to be applied)*: any saproxylic invertebrate population or assemblage.
2. *Intervention (i.e., the policy or management action under scrutiny)*: any site-based management action.
3. *Outcome*: desired primary outcomes were change in population density for a target species or change in species richness within assemblages.

3.2 Search Strategy

Relevant studies were identified through computerised searches of the following electronic databases:

- ISI Web of Knowledge
  - ISI Web of Science: Science Citation Index Expanded (1945-present)
  - ISI Proceedings: Science and Technology Proceedings (1990-present)
- JSTOR

- Science Direct
- Directory of Open Access Journals (DOAJ)
- Copac
- Scirus
- Scopus
- Index to Theses Online (1970-present)
- Digital Dissertations Online
- Agricola
- CAB Abstracts
- English Nature's "WildLink"
- Countryside Council of Wales (CCW) library

The search terms used were:

- Saproxylic
- Coleoptera AND conservation
- Diptera AND conservation
- Dead AND wood AND invertebrate*
- Over mature AND tree AND invertebrate*
- Over-mature AND tree AND invertebrate*
- Fallen AND wood AND invertebrate*
- Pollard AND invertebrate*
- Brash AND conservation AND invertebrate*

Publication searches were also conducted using the internet meta-search engines Alltheweb and Google Scholar; the first 50 word document or PDF hits from each website were examined for appropriate literature and data. In addition, the following statutory organisation websites were inspected: UK Department for Environment, Farming and Rural Affairs (Defra), Northern Ireland Department of Agriculture and Rural Development (DARD) and European Union portal (Europa). The specialist publication "Coleopterist" was searched by hand for any appropriate information. Bibliographies of articles accepted into the systematic review at the full text stage and traditional literature reviews were searched for studies that had not yet been identified by any other means. Recognised experts and practitioners were contacted and asked to recommend any additional sources of potentially relevant information.

The systematic review identified studies conducted in North America and Europe, although specific non-English language searches were not performed. All suitable material was included into the start of the systematic review process, irrespective of geographic location.

3.3 Study Inclusion Criteria

Studies were initially filtered by title and any obviously irrelevant articles were removed from the list of captured articles. Subsequently, the abstracts of the remaining studies were examined with regard to possible relevance to the systematic review question. A subset of approximately 10% of these articles (n = 75) was also assessed for relevance by a second independent reviewer; agreement on inclusion between the reviewers was deemed to be "substantially good" (Cohen's Kappa test: K = 0.71). Studies were accepted for viewing at full text if it appeared that they may contain information pertinent to the review question, or if the abstract was ambiguous and did not allow inferences to be drawn about the content of the article (i.e., if there was insufficient information to determine that the study was inappropriate for systematic review).

The criteria, which studies had to meet for inclusion into the final stage of the systematic review, were:

1. *Subject*: any saproxylic invertebrate population or assemblage.
2. *Intervention*: any site-based management action.
3. *Outcome*: desired primary outcomes were change in population density for a target species or change in species richness within assemblages. Nonetheless, studies were not rejected on the basis of outcome.
4. *Type of study*: any. No comparator was necessary for inclusion, although appropriate spatial or temporal controls were a prerequisite for studies to be included in any subsequent meta-analysis.

Studies accepted into the review at full text were considered for relevance by two additional independent reviewers. Any disagreement on inclusion was discussed and resolved by consensus.

3.4 Study Quality Assessment

Study quality assessments were not performed on the studies accepted into this systematic review. This was because the quality of the studies fell below the *a priori* defined quality threshold and the review does not, therefore, include quantitative synthesis.

3.5 Data Extraction & Data Synthesis

Any information related to the systematic review question was extracted from the studies and collated in qualitative tables. The variation in type of investigation and range of outcome measures adopted in the studies precluded the use of formal statistical techniques. Direct comparisons between studies of saproxylic species must be made with caution, as different sampling techniques can provide a bias overview of the assemblage. For example, free hanging window traps will not collect species that are unable to fly, and the composition of the sample may be affected by factors such as the flight activity of species and random drift in flight due to air currents. However, compared to other sampling methods, such as trunk traps, they yield a greater range of species (Siitonen 1994; Økland 1996; Similä et al. 2002b), although rare and threatened species are often under represented (Økland 1996; Muona 1999; Martikainen 2000).

4. RESULTS

4.1 Review Summary Statistics

Searching was completed in December 2005. Two hundred and eighty six studies remained in the systematic review after the abstract filter stage (Table 1); 239 were captured using electronic database searches and 47 were found via other sources. Thirty two of the 286 studies could not be obtained at full text for further examination, as they were unavailable from the British Library and the author(s)/publisher. In addition, a further 10 articles could not be located due to bibliographic errors and four references are awaiting translation to English.

Table 1: Number of studies included during each of the systematic review filtering stages.

Systematic review stage	**No. of studies**
Studies captured using search terms in electronic databases* (including duplicates)	6867
Studies captured using search terms in electronic databases* (excluding duplicates)	5841
Studies remaining after title filter	791
Studies remaining after abstract filter	286
Studies remaining after full text filter	95

* *(excludes studies captured in English Nature's WildLink database and hits from internet searches)*

Over 90 studies were examined at full text for information relating to the impact of specific site-based management interventions on the saproxylic invertebrate fauna. However, much of this literature consisted of either species inventories for specific sites or comparisons of the relative success of various trapping techniques. Consequently, only 26 of these studies satisfied the inclusion criteria and were accepted into the systematic review.

4.2 Outcome of the Review

None of the studies examined at full text report changes in the long-term persistence of saproxylic populations, or in species richness within assemblages, as a direct result of specific site-based management interventions. Hence, we conclude that there is insufficient robust data from long-term fully replicated and controlled field-based experiments, or investigations, to definitively evaluate the effectiveness of current management recommendations. Although this type of evidence is lacking, there are studies that provide relevant information on the influence of various habitat management actions on the saproxylic fauna. However, the dissimilarity in type of investigation and range of outcome measures adopted in the studies precluded the use of formal statistical techniques.

The 26 studies were divided into two groups. The first group consisted of studies that investigated the saproxylic invertebrates in managed (e.g., clear-cut or thinned) and unmanaged sites (e.g., mature or ancient forest). The second group compared the saproxylic assemblages associated with different types of specific management intervention (e.g., the provision of different types of supplementary CWM or the creation of canopy gaps). The vast majority of studies focused specifically on saproxylic beetles, although other taxonomic groups were represented. Please refer to Appendix Two and Three, respectively, for a breakdown of the methodology and results for each individual study.

4.2.1 Saproxylic invertebrates in managed and unmanaged wooded habitats

The results of many of the studies are contradictory. For example, Martikainen et al. (2000) and Sippola et al. (2002) recorded greater numbers of species in old-growth forest than in managed woodland, whereas Väisänen et al. (1993) and Kaila et al. (1997) established the opposite trend. Other inconsistent findings have also been recorded for investigations into the distribution of species within the CWM on sites; Sverdrup-Thygeson & Ims (2002) noted higher numbers of species utilising snags as substrate rather than logs, yet Väisänen et al. (1993) documented more species associated with logs. Nonetheless, several clear trends are evident throughout the studies. For instance, rare saproxylic species were consistently recorded at relatively higher abundance within unmanaged old-growth forest compared to managed woodland (Väisänen et al. 1993; Similä et al. 2002a; Sippola et al. 2002; Similä et al. 2003). In addition, managed and unmanaged wooded habitats support different saproxylic assemblages, some species of which are threatened specialists found exclusively within each respective type (Kaila et al. 1997; Martikainen et al. 2000; Similä et al. 2002a; Similä et al. 2003; Hammond et al. 2004).

4.2.2 Impact of specific management interventions on saproxylic invertebrates

A small number of studies examined the impact of specific site-based management interventions on saproxylic invertebrate communities. Alexander (1999) found that branch wood left to decay in the sun had a very different saproxylic assemblage to that left to decay in the shade, with each treatment group having an associated specific rare specialist fauna. Another study investigating the influence of sun-exposure found that species richness was higher in logs, irrespective of the level of shade experienced, than in artificially provided high stumps (Wikars et al. 2005). The creation of canopy gaps can also impact saproxylic species abundance and diversity by altering the degree of sun-exposure within a forest (Ulyshen et al. 2004). Small canopy gaps had a lower diversity of species than larger ones, but gap size did not significantly affect saproxylic beetle abundance. However, species abundance and diversity were significantly higher in younger gaps when compared to older gaps.

A control trial evaluating simulated “logs” and natural logs as substrates for saproxylic invertebrates recorded comparable numbers of individuals on the different types of substrate, although the number of species per simulated log was lower (Fager 1968). Nevertheless, enrichment of the artificial substrate increased both the number of individuals and species in the simulated logs.

Hammond et al. (2001) compared the saproxylic fauna on artificially provided aspen (*Populus tremuloides*) CWM and found that snags had a more diverse early successional assemblage than either stumps or logs. A second study comparing aspen CWM of different construction concluded that the number of species found on naturally formed and man-made high stumps was very similar, but that the natural stumps had greater numbers of red-listed species present than the new dead wood (Jonsell et al. 2004).

5. DISCUSSION

The objective of this systematic review was to collate and synthesise published and unpublished evidence in order to evaluate the effectiveness of current management recommendations for conserving saproxylic invertebrates. Unfortunately, insufficient robust, high quality evidence (i.e., data from long-term fully replicated and controlled field-based experiments or investigations) was found to definitively appraise the success of interventions for a particular saproxylic species or community. None of the studies demonstrate either a positive, or a negative, effect on long-term population persistence, or species richness within an assemblage, as a direct result of a specific site-based management action. However, there is some evidence describing positive changes in the saproxylic fauna in response to a range of management practices, observed over relatively short periods of time. The research also suggests that employing a variety of different management interventions will maximise microhabitat heterogeneity and, therefore, the diversity of species present on a site.

At this stage, we cannot reject the hypothesis that the long-term stability and persistence of saproxylic invertebrates can be facilitated by incorporating management interventions, such as the provision of supplementary dead and decaying wood, into site management plans. General recommendations for the maintenance of suitable microhabitats, such as the protection of veteran trees within the landscape, are based on sound ecological principles and should not be discouraged even though experimentally rigorous evidence is lacking. For instance, common sense dictates that species associated with oak decay will not thrive if living oak trees that are decaying are felled or fallen wood is cleared away from a site. Equally, it must be appreciated that the best available evidence is inadequate to draw firm conclusions with regard to the optimum use of different interventions in specific circumstances (e.g., when constrained by a limited budget, would the provision of supplementary logs or high stumps be a more effective tool to conserve saproxylic communities in aspen dominated woodland?). There are still substantial gaps in our knowledge about the efficiency of these management practices, especially in relation to the explicit impacts they will have on particular taxonomic groups.

There are considerable difficulties and ethical stumbling blocks in the undertaking of robust primary research on such a topic, which may give reason to their paucity. Large numbers of confounding variables operate in such complex ecological systems and it is hard to find suitable analogous controls in close proximity within a study area (i.e., two woodlands with the same saproxylic assemblage present prior to implementing different management actions, that are otherwise experiencing similar abiotic and biotic pressures). In addition, temporal experimentation might necessitate activities that are detrimental or inappropriate for the conservation of species (e.g., the destruction of microhabitats to determine species presence/absence), resulting in a conflict of interest between knowledge acquisition and conservation. The highly complex and varied life-histories of saproxylic invertebrates make them an inherently difficult taxonomic group to study.

The contradictions evident in the results of studies comparing the saproxylic fauna of managed and old-growth wooded habitats may be attributed to a number of factors. First, the authors rarely provide full definitions for the terminology they have adopted within a publication. This is exacerbated by debate among subject experts in relation to when certain terms, such as "old-growth", should be used (see Butler et al. 2001 for a review). For example, "unmanaged woodland" may or may not be enclosed and therefore subject to different pressures from wild or domesticated grazing herbivores. Second, the variation in experimental scale and trapping methodologies could cause inconsistencies in results across studies, especially as the microhabitats that species occupy may be very small. For instance, in old growth forests, traps placed in close proximity to living veteran trees may collect different fauna to those located on fallen dead wood (B. Dodelin personal communication).

5.1 Implications for Management

5.1.1 Promoting the value of veteran trees & old-growth wooded habitats

In recent years, there have been considerable advances in our ecological understanding of the communities dependent on dead and decaying wood microhabitats (Speight 1989; Alexander 1998). Dead wood has a limited existence and is an ephemeral habitat. It decomposes over time, with new microhabitats continually evolving, maturing and increasing in both complexity and suitability for a diverse range of saproxylic species. The most important substrates are veteran trees which, over many years, acquire columns of decay in the dead heartwood, or centre of the trunk, and act as refugia for specialist saproxylic invertebrates confined to stable old-growth decay microhabitats (Read 2000, Alexander 2004). This conclusion was apparent in the findings of this systematic review, with high numbers of rare specialist species being consistently recorded within unmanaged old-growth (Väisänen et al. 1993; Similä et al. 2002a; Sippola et al. 2002; Similä et al. 2003).

In Europe, there has been an increasing recognition of the value of veteran trees and ensuring their perpetuity has become a significant conservation objective (Speight 1989; Harding & Alexander 1993; Harding & Alexander 1994; Nilsson & Baranowski 1994; Fowles et al. 1999; Read 2000; Alexander 2004). Continued endorsement of the value of these trees, particularly by ecological organisations such as the Ancient Tree Forum (ATF) and the Veteran Tree Initiative (VTI), is a vital component of current saproxylic conservation strategies. Active management and education is required to prevent further declines as a direct result of neglect and ignorance (e.g., grazing animals may strip bark from trees which can lead to premature death), thus prolonging the lives of veteran trees and providing time for new generations to be brought on. In addition, this is supported by objective frameworks, the Saproxylic Quality Index (SQI) and Index of Ecological Continuity (IEC), used to rank the importance of sites and aid appropriate designation and the allocation of limited conservation resources (Speight 1989; Harding & Alexander 1993; Fowles et al. 1999; Alexander 2004).

5.1.2 Encouraging microhabitat heterogeneity

Ordinarily, there are numerous specialist niches along environmental gradients for saproxylic species to exploit and many species are adapted to survive within specific successional stages within an ecosystem (Jonsell et al. 1998; Martikainen 2001; Similä et al. 2002a). Current recommendations for saproxylic invertebrate conservation encourage management strategies that maximise microhabitat diversity on sites (Cavalli & Mason 2003). Habitats, such as woodland and parkland, should therefore be adequately endowed with both a spatial and temporal continuity of dead and decaying wood, including veteran trees and a diverse selection of standing and fallen CWM subject to a range of different abiotic conditions. This will increase the diversity of available dead wood microhabitats and microclimates necessary to ensure the long-term stability and preservation of a saproxylic community on a site (Speight 1989; Fry & Lonsdale 1991; Alexander 1993; Kirby 2001; Cavalli & Mason 2003; Alexander 2004).

The limited available empirical evidence collated in this systematic review supports maximising microhabitat heterogeneity by artificially varying the orientation, and type, of CWM on a site. For example, different saproxylic faunas benefit from CWM left to decay in the sun and in the shade (Alexander 1999) and species diversity positively responds to the creation of large canopy gaps (Ulyshen et al. 2004). Furthermore, the results of the studies were inconsistent in regard to which construction of CWM harboured the greatest number of species (Väisänen et al. 1993; Hammond et al. 2001; Sverdrup-Thygeson & Ims 2002; Wikars et al. 2005), so it would be pertinent to provide a range of logs, snags and stumps for the saproxylic fauna to utilise.

5.1.3 Significance for best-practice for forest management

There is a deep-rooted aversion towards dead wood among European foresters and land managers, which is likely to be a product of their training (Speight 1989; Winter 1993). Nevertheless, attitudes are beginning to change and there is a growing awareness that commercial forestry should not preclude the conservation of saproxylic invertebrates (Cavalli & Mason 2003). Frequently, the profit made from selling timber does not cover the cost of harvesting and, in such circumstances, foresters are now more likely to leave timber in clear-cut areas for the benefit of the saproxylic fauna. However, care must be taken to make sure that these CWM substrates are not subsequently destroyed during future felling activity (e.g., logs are often fragmented by mechanical operations). In addition, the CWM must be regularly replenished as logging waste is usually small in diameter and therefore decomposes relatively quickly (Bader et al. 1995).

The limited available evidence obtained in this systematic review verified that managed (e.g., clear-cut or thinned) sites, where dead and decaying trees and CWM were retained, harboured a different saproxylic assemblage to that in unmanaged forest areas, and that some species present in clear-cuts were rare specialists exclusively associated with early successional dead wood habitats (Kaila et al. 1997; Martikainen et al. 2000; Similä et al. 2002a; Similä et al. 2003; Hammond et al. 2004). Where economically viable, species diversity could therefore be increased in plantation forests by provision of CWM substrates in clear-cut areas and the strategic planting trees of varying age in order to reduce the uniformity of the stand (Linder & Östlund 1992; Haila 1994). Results from the studies also suggested that some threatened saproxylic species can actually tolerate clear-cutting if sufficient suitable living and dead trees are retained (Martikainen 2001; Sippola et al. 2002; Similä et al. 2003).

Even though these practices are already being implemented to mitigate the effects of commercial forestry, the uniform stand structures formed in previous decades will continue to dominate the landscape in the years to come. As many saproxylic species are highly sensitive to forest disturbances and management regimes (Heliövaara & Väisänen 1984; Speight 1989, Martikainen 2001), they can serve as useful indicators of forest sustainability and ecosystem recovery.

5.2 Implications for Research

A majority of the studies accepted into this systematic review are from Scandinavia and have been conducted in forest environments. Despite the widely acknowledged importance of historic parklands and open pasture-woodland in Britain, very few experimentally rigorous research projects have been carried out in these habitats and it cannot be assumed that lessons learnt from investigations in extensive forest areas are transferable to open habitats. Primary research projects targeted within these habitats would be valuable in order to substantiate the current management guidelines for the site-based conservation of saproxylic invertebrates in Britain.

Indeed, on examination of the studies included in this systematic review, little could be inferred with regard to which specific species would directly benefit from any particular site-based management intervention. Further research is therefore much needed to assess the optimum state and critical quantities of dead and decaying wood substrate that should be provided in order to sustain and preserve saproxylic assemblages.

In many investigations, CWM is categorised by construction (i.e., snag, log or stump) and decay class. These decay classes are generally based on physical characteristics and may be poor descriptors of the actual state of decomposition. For example, units of CWM are commonly categorised by the percentage bark cover still remaining on the substrate. However, such measures are very coarse and not indicative of the fauna present, as any class may span many years and different stages of decomposition (Esseen et al. 1992; Esseen et al. 1997). It would therefore be more instructive to use biologically meaningful classifications, such as the type and extent of heart rot present in the CWM or the degree of sunlight that it has been exposed to. Considering the provision of supplementary CWM alone, independently of the complex interactions that occur between species within a woodland ecosystem, is not sufficient to guarantee the long-term persistence of saproxylic species. A more holistic approach needs to be adopted as additional factors, such as abundance of nectaring resources for insects or the specific nature of fungal-insect associations, may also limit survival (Wallace 1954; Lawrence 1989; Ahnlund & Lindhe 1992; Cavalli & Mason 2003; Cheesman & Wilde 2003; Alexander 2004).

The effectiveness of conservation interventions for saproxylic species must be monitored long-term. For instance, the impact of an artificial increase of CWM on the saproxylic fauna will not be discernable in a normal 3 year study period, as the dead material will not have reached the decomposition state necessary for colonisation by secondary species associated with the later stages of decay. To fully understand the contribution of the CWM, the supported saproxylic assemblage needs to be regularly sampled until the dead wood is entirely degraded and is no longer a suitable substrate.

Although, over recent decades, information on the habitat associations of many species has been published within the specialist literature (e.g., Alexander 2002), further detailed autecological research for saproxylic invertebrates, particularly those under threat, is required in order to improve the efficiency of conservation management action on sites (Paviour-Smith & Elbourn 1993; Fowles et al. 1999; Rotheray et a;. 2001; Cheesman & Wilde 2003). However, once determined, conservationists often assume the habitat requirements of a species to be constant and manage habitats to maintain these conditions. For many species, these requirements are likely to change in response to climate warming, and care must be taken not to manage habitats based on outdated prescriptions (Davies et al. 2006). Therefore, maintenance of a heterogeneous range of microhabitats will help to buffer saproxylic populations and communities against environmental change.

Another cornerstone in the successful conservation of saproxylic invertebrates is an awareness of where different species exist at both a within-habitat and landscape scale. For this purpose, site inventories are crucial. Traditionally, entomological recording has been focused around the more rewarding sites but, more recently, previously ignored and undiscovered sites have been searched and well documented (Alexander 2004). Knowing which threatened species are present on a site will inform conservation management decisions, such as which tree species should dominate the dead and decaying wood substrate or be planted in order to ensure new generations in the future (Key & Ball 1993). A better understanding of the distribution of species, at different spatial scales, will also allow practitioners to allocate conservation resources in order to increase habitat connectivity (Alexander 2004). Historically, the range of many European saproxylic species can be traced back to the former distribution of forest and woodland. Anthropogenic modification of the landscape has led to the increasing isolation of relict habitat fragments and, consequently, increased the probabilities of extinction for the species that inhabit them (Hanski 2000). Saproxylic species are also vulnerable to within-site fragmentation due to their generally limited dispersal capabilities (e.g., Ward 1987; Ranius 2000; Ranius & Wilander 2000; Alexander 2003; Brunet 2003). Artificially providing units of dead wood substrate in close proximity to one another may reduce the risk of local extinction for vulnerable species and even potentially facilitate new colonisations (Key & Ball 1993; Alexander et al. 1996; Schiegg 2000; Butler et al. 2002; Cavalli & Mason 2003; Alexander 2004).

There is a profusion of important information, relating to the ecology and occurrence of saproxylic invertebrates, recorded in the notebooks of experienced amateur and professional entomologists (Fowles et al. 1999). Dissemination of this invaluable data to a wider audience is vital for the conservation of saproxylic species and may well prevent duplication of research effort by independent parties. We therefore urge such individuals to commit their knowledge to paper, whether in the peer-reviewed literature or specialist group publications. The principle aim for entomologists and conservationists in the future must be to assemble the high quality evidence-base necessary to enable policy makers, and practitioners, to make informed decisions with regard to dead wood protection and provision, in order to facilitate the successful conservation of saproxylic invertebrates.

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Appendix One: list of publications providing conservation management guidelines for saproxylic invertebrate conservation

Alexander, K.N.A., Green, E.E. & Key, R.S. (1996). *The Management of Over Mature Tree Populations for Nature Conservation – the basic guidelines*. In Pollard and Veteran Tree Management II, ed. H.J. Read, pp.122-135. Corporation of London, London, UK.

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Appendix Two: studies investigating the saproxylic fauna in managed and unmanaged sites

Study	**Country**	**Taxonomic Group(s) and No. of Species (*conservation status*)**	**Habitat**	**Brief Summary of Methods**	**Brief Summary of Results**
Hammond et al. (2004)	Canada	A saproxylic beetle assemblage 257 taxa, mostly identified to species level (*not stated*)	Trembling aspen (*Populus tremuloides*) dominated stands, which also contained balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*) and birch (*Betula papyrifera*).	A comparison of saproxylic assemblages in different aged stands: 1. old (>100 years) 2. mature (60-90 years). Three classes of decaying coarse woody material (CWM) were examined: 1. low: >90% bark coverage (snags with few or no leaves, many twigs, >20 limbs longer than 1m; logs with <10% plant coverage, <10% cross-sectional area showing decay) 2. medium: 60-90% bark coverage (snags with no leaves, few or no twigs, 5-20 limbs longer than 1m; logs with 10-30% plant coverage, 10-50% cross-sectional area showing decay) 3. high: <60% bark coverage (snags with no leaves, no twigs, <5 limbs longer than 1m; logs with >30% plant coverage; >60% cross-sectional area showing decay) Snags were divided into 5 size classes based on breast diameter: 1. <11cm 2. 11-20.9cm 3. 21-30.9cm 4. 31-40.9cm 5. >40.9cm One snag and one log of each decay class were sampled in each stand. Beetles were sampled using bolt cuts and window traps. Fauna from the bolt samples were reared and collected for 2 years between Apr to Sep. Fauna from window traps on the snags was emptied between May and	Twice the number of individuals and 34% more species were reared from CWM in old stands rather than mature stands. However, standardised species richness (abundance standardised to the largest wood volume) did not differ between stands of different ages. Stand age had no effect on mean abundance or species richness for window trapped beetles. Faunal similarity between old and mature stands was 68% window trapped beetles and 49% for CWM reared beetles. Of the 257 taxa collected, 54 “rare” species (<10 specimens each) were collected exclusively from old stands. 10 species were significant indicators of old stands. 44 species were only found in mature stands, 3 of which were considered to be significant indicators. Mean abundance did not significantly differ among decay classes. However, there was a trend towards greater numbers of individuals in low decay CWM, but species diversity was lower than in highly decayed CWM. Beetle assemblages were 60% similar between logs and snags. 47 species were unique to logs or snags.

				Oct, then May to Aug the following year.	Diameter of CWM is likely to reflect age of stand, although overlap was observed. The number of rare species tended to increase with increasing snag diameter, and the number of unique species peaked in the 21-30.9cm class. However, there was at least one unique species for each class. There were 15 indicator species for the larger diameter snags, whereas only 4 species indicative of other diameter classes.
Hövemeyer & Schaermann (2003)	Germany	A Dipteran assemblage. The number of saproxylic species present was not stated. (*not stated*)	Beech (*Fagus sylvatica*) dominated forest	A 10 year investigation of the saproxylic fauna of branch wood from dead beech trees. Eleven branches (4.3-11.5cm in diameter), from 2 felled beech trees, were sawn into 65 logs (approx 30cm long). Diameter and volume were measured prior to exposure. Logs were then arranged on a grid on the forest floor. Sampling started 2 years after initial exposure. 6 logs were examined and the following variables recorded: 1. % bark cover 2. % litter cover 3. % moss cover A vertical hole, 1cm diameter, was drilled through each log. The bore-meal was weighed fresh and dried (4 days at 60 ^{o}C) to determine water content, then analysed for carbon and nitrogen content. Each log was finally placed in an emergence trap. Samples were collected three times a year, for 2 years: summer (Jun/Jul), autumn (Sept/Oct) and spring (Mar/Apr the following year). This sampling procedure was repeated for 9 years.	Saproxylic species were positively affected by high water content in the branch wood.
Kaila et al. (1997)	Finland	A saproxylic beetle assemblage 129 species (*not stated*)	Two mixed forests between 70-80 years old, with a tree canopy cover of 70-85%	A comparison of saproxylic beetle assemblages on dead birch trunks within 2 forests with: 1. a closed, mature forest area (14 traps in forest one; 11 traps in forest two) 2. an open, recently clear-cut area (<5 years ago) with some decaying birch left behind (14 traps in forest one; 11 traps in forest two).	DCA ordinations showed clearest variation in beetle assemblage between closed versus open forest areas; both types of forest area harboured different beetle faunas. There was no difference in the number of beetles in the clear-cut and mature forest areas.

			Forest one: 40% birch and 60% Scots pine Forest two: 7-28% birch, 0-79% Scots pine and 5-93% Norway spruce	One forest area was also examined before and after clear-cutting (3 years later) and compared to an independent control area of non-managed mature forest. To minimise variation caused by different species of fungi, the study was limited to white-rotted birch trunks Samples were collected using trunk window traps between May and Oct.	The number of species was significantly higher in the managed forest area after the clear-cut. However, clear-cutting resulted in reduced median sample sizes. The median number of species remained the same in the mature forest control area, before and after cutting in the managed forest area. Rare beetles were recorded in the clear-cuts and *Denticollis borealis* was only found in these areas. The threatened species *Triplax rufipes* and *Carphacis striatus* were found in mature forest only.
Martikainen et al. (2000)	Finland	A beetle assemblage consisting of: 553 species in total. 232 of which were saproxylic species (*not stated*)	Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated forests	A comparison of the beetle fauna in different age classes of forest: 1. mature (95-120 years old, cut stumps abundant) 2. over-mature (>120 years old, cut stumps abundant) 3. old-growth (>160 years old, no or few cut stumps present) 1ha sample areas were established in each stand: 10 plots in mature forest, 11 in over-mature forest and 9 in old-growth forest. 15 stand characteristics were measured in each sample plot. 10 window traps were used to sample the beetle fauna in each plot between Apr and Sep.	Saproxylic species richness was significantly higher in old-growth forests than in managed forests. 78% of saproxylic beetles were more abundant in old-growth forest than managed forest and the species assemblages had limited overlap. There were positive correlations between the total number of saproxylic species and 90% of the measured dead wood characteristics. The strongest relationship was with the total volume of dead wood (which was highly intercorrelated with other ecological variables).
Moretti et al. (2004)	Switzerland	A arthropod assemblage, including the following saproxylic beetle families: Cerambycidae Buprestidae Lucanidae (*not stated*)	Alpine forest	An investigation of the affect of forest fires on arthropod diversity in an 11 x 15km area. Sites were categorised into 3 classes of fire frequency during a 30 year period: 1. Burnt once (n = 8) 2. 3-4 burns (n = 8) 3. Unburnt control Tree canopies were more open and the grass cover was greater on sites that had been burnt. The diameter, at breast height, of dominant trees was also smaller.	Fire had a positive effect on species richness within these beetle families, although this trend was not statistically significant. *Chlorophorous figuratus* and *Stenopterus rufus* were only found in sites that had been burnt. *Leptura maculate* and *Agrilus angustulus* favoured repeated fires, but were found in sites of all 3 classes of fire frequency.

				Window and yellow traps were used to sample saproxylic fauna. One trap of each type was installed at every site. Traps were emptied between Mar and Sep.	
Økland et al. (1996)	Norway	A saproxylic beetle assemblage 194 species (*21 Norwegian red-listed species*)	Norway spruce (*Picea abies*) dominated forest	An investigation into the influence of 35 ecological variables on a saproxylic assemblage, at different spatial scales. These variables included factors relating to the decaying wood present, wood inhabiting fungi, level of disturbance, landscape ecology and surrounding vegetation structure. The landscape was examined at 3 different spatial scales: 1. small: 0.16ha plots (n = 49) 2. medium: $1km^2$ areas, grouping together 2-3 of the 0.16ha plots (n = 17) 3. large: $4km^2$ areas, grouping together 0.16h plots (n = 9) All of the small plots had the same characteristics: 1. forest age was >80 years 2. different amounts of decaying wood and levels of disturbance were represented 3. a minimum distance of 200m between the sites. 10 window traps used per plot and were emptied between Apr and Sep.	Only dead wood and wood inhabiting fungi related variables had a significant effect on species richness, across all spatial scales. However, many of these variables were highly intercorrelated. Former clear-cutting had a negative effect on species richness at a large spatial scale only.
Ranius & Jansson (2000)	Sweden	A saproxylic beetle assemblage 120 species (*48 Swedish red-listed species*)	Forests with high densities of oak (*Quercus robur*) trees present	An investigation of the saproxylic beetle assemblages associated with oak forest and hollow tree characteristics. The beetle fauna of 5 living, hollow oak trees in 18 (0.5-0.8ha) plots was surveyed, between May and Aug, using pitfall and window traps. Plots were assessed for the following habitat variables: 1. vertical extent of original canopy cover (10-30%, 30-70% or 70-90%) 2. forest re-growth (grazed or natural regeneration) 3. stand size (small or large) Each tree hollow was assessed for: 1. amount of wood mould (small or large)	Species richness was greatest in plots with large, free standing trees. Large girth and low canopy cover increased frequency of occurrence for several species. Forest re-growth was detrimental for many species. Red-listed species showed the same trends in occurrence as other species.

				2. area of entrance (cm^2) 3. surrounding cover (free-standing, semi-shaded or shaded) 4. sunshine direction (direction of entrance in relation to the sun) 5. vertical orientation of hollow (horizontal or upwards, either vertical or oblique) 6. height (ground level to entrance hole in m) 7. trunk diameter (in cm, at a height of 1.3m)	
Ranius (2002)	Sweden	A saproxylic beetle assemblage 47 species (*20 Swedish red-listed species*)	Stands with decaying hollow oaks (*Quercus robur*).	An investigation of the saproxylic assemblages in standing oak trunks. Most of the trunks surveyed were alive (only 2 were dead). Physical characteristics, associated with microclimate and successional stages, were measured for each tree: 1. aspect (direction of entrance to sunshine) 2. canopy cover (unshaded with a canopy cover of <75%; shaded canopy with >75% cover) 3. entrance (horizontal or upwards, either vertical or oblique) 4. height (ground level to entrance hole in m) 5. size of opening (cm^2 log-transformed) 6. stand size (as above) 7. trunk diameter (in m, at a height of 1.3m) Samples of wood mould were collected from one opening in each tree. These samples were searched for larvae and beetles (including specimen fragments). Only saproxylic beetles specifically associated with tree hollows were recorded. Presence/absence of each beetle species was examined in relation to the variables.	Many species tended to be more frequent in larger trunks, but this was only significant for *Tenebrio opacus* and *Procraerus tibialis*. However, the latter also occurred in the smallest trees (minimum diameter of 0.35m), though at low frequencies. No species showed a preference for shaded or unshaded trees. Most species tended to be absent from hollows with an entrance directed upwards. This was a significant trend for *Ampedus cardinalis*, *Ampedus hjorti* and *Allecula morio*. Species richness was greater in hollows situated higher up the tree. This was a significant trend for *Ampedus cardinalis*, *Elater ferrugineus*, *Prionychus ater* and *Liocola marmirata*. Species richness per tree increased with increasing stand size. Only *Elater ferrugineus*, *Osmoderma eremite* and *Tenebrio opacus* were significantly associated with large stands.
Schiegg (2001)	Switzerland	A saproxylic assemblage consisting of: 426 Diptera 228 Coleoptera (*66 Swiss red-*	Beech (*Fagus sylvatica*) and Noway spruce (*Picea abies*) dominated forest, which also contained	A comparison of the saproxylic fauna on beech trunks and limbs. Insects were collected in 14 study plots, within a $10km^2$ forest reserve, using four emergence traps per plot; two of these traps were placed on trunks and two on limbs. Samples were emptied between Apr and Nov.	Limbs harboured more species and had a higher diversity than trunks for both taxonomic group of saproxylic insect. 60 beetle species collected from the trunks and 66 species collected from the limbs were red-listed.

		listed beetle species)	ash (*Fraxinus excelsior*) and fir (*Abies alba*) trees		82.6% of saproxylic beetles and 55.3% of saproxylic Diptera were present in both trunks and limbs.
Siitonnen & Saaristo (2000)	Finland	The saproxylic beetle species *Pytho kolwensis* (*on the Finnish and Swedish red-list*)	A Norway spruce (*Picea abies*) dominated forest, which also contained Scots pine (*Pinus sylvestris*), birch (*Betula* spp.) and aspen (*Populus tremula*)	An investigation into how the presence/absence of *P. kolwensis* was related to host tree (spruce) and stand characteristics. *P. kolwensis* larvae were sampled from 2-15 years old spruce logs, showing signs of decay (e.g., peeling strips of bark from the basal part of the log). The quality of 145 potential host trees was assessed by measuring: 1. trunk diameter (in cm, at a height of 1.3m) 2. bark cover (%) 3. epiphyte cover (%) 4. wood softness (mean knife penetration depth) 5. mycelium cover (%) 6. trunk height (median height from ground level) Stand characteristics were measured at six study areas ranging from 4.3 to 7.8ha in size. Five 25 x 25m plots were laid out in each stand and the following variables were recorded: 1. amount of living and dead wood 2. stand age 3. decay class 4. condition of dead wood 5. volume of dead wood and live trees present	55 of the sampled host trees were inhabited by *P. kolwensis*. 87% of trees hosting *P. kolwensis* had a trunk diameter of >20cm, >50% bark cover, >1.5cm knife penetration depth, <75% mycelium cover, and the trunk had not been in continuous contact with the ground. All *P. kolwensis* habitat was virgin spruce-mire forest with a stand continuity of at least 170-300 years old and a high volume of dead wood (73-111m^3ha^{-1}).
Similä et al. (2002a)	Finland	A beetle assemblage. The number of saproxylic species present was not stated. (*12 Finnish red-listed saproxylic species*)	Scots pine (*Pinus sylvestris*) dominated forest	A comparison of beetle species assemblages between managed and semi-natural forest areas in 5 stages of forest succession: 1. sapling (clear-cut or burnt 7 years ago) 2. young (~40 years old) 3. middle-aged (~70 years old) 4. mature (~110 years old) 5. old-growth (>150 years old) Three replicate plots were identified in both managed and	Semi-natural and managed forests contained different assemblages of saproxylic insects. The earliest stage successional forests harboured different species assemblages to the later stages. The number of rare saproxylic species was higher in semi-natural forests than managed forests, although this trend was not statistically significant.

				semi-natural forest, for each of these successional stages. Beetles were sampled with window traps (5 traps per plot) between May and Sep.	
Similä et al. (2003)	Finland	A saproxylic beetle assemblage 186 species (*33 Finnish red-listed species*)	Scots pine (*Pinus sylvestris*) dominated forest	A comparison of the saproxylic beetle assemblages found in managed and semi-natural forests. The stands of managed and semi-natural forest were classified into 4 successional types: 1. young (~40 years old) 2. middle-aged (~70 years old) 3. mature (~110 years old) 4. old-growth (>150 years old) Three replicate plots were identified in both managed and semi-natural forest, for each of these successional stages. The following habitat variables were recorded: 1. type of dead wood (standing snag or log) 2. decay state of dead wood (recent, intermediate, high decay) 3. volume of dead wood Beetles were sampled with window traps between May and Sep.	136 species found in managed forests and 147 in semi-natural forests; 52% of species were common to both forest types, 21% restricted to managed stands and 27% restricted to semi-natural stands. Bark beetles (23 species) were more abundant and diverse in semi-natural forests, although this was not statistically significant. Bark beetle species richness was positively related to the volume and diversity of dead wood. The assemblages of other saproxylic beetles were different between semi-natural and managed forests. In managed forests the diversity and volume of dead wood were positively correlated with species richness. This trend was not observed in semi-natural forests. Species richness for the 33 red-listed was greater in semi-natural forests and was positively correlated with volume of decayed wood and diversity of dead wood.
Sippola et al. (2002)	Finland	A saproxylic beetle assemblage 180 species (*2 Finnish red-list species, 29 nationally rare species*)	Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated forests	A comparison of saproxylic beetle fauna in six different types of forest: 1. old-growth dominated by pine 2. old-growth dominated by spruce 3. old-growth dominated by spruce, with various deciduous trees 4. managed 1 year-old seed-tree cut pine forest 5. managed 15 year old seed-tree cut pine forest 6. managed 15 year old clear-cut spruce forest 28 plots (1-0.5ha) were established in the 6 forest types. 28 environmental variables relating to living tree cover, dead wood features and site characteristics were measured in	Species richness was higher in old-growth forest areas than in managed forest areas. There was no difference in species richness between pine and mixed forests, nor between any of the cutting treatments. More rare saproxylic species were found in old-growth forest than in cut forests. Species richness correlated positively with measures of dead wood availability and site fertility (volume of living trees and % cover of eutrophic plants).

				each plot. Beetles were sampled by window trapping between Jun and Sep. Five traps were used in each sample plot.	
Sverdrup-Thygeson & Ims (2002)	Norway	A saproxylic beetle assemblage 232 species (*18 Norwegian red-listed species*)	A Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated forest, which also contained birch (*Betula* spp.) and aspen (*Populus tremula*)	A comparison of the saproxylic beetle assemblages found on naturally occurring aspen snags and logs, experiencing varying degrees of sun-exposure, across a gradient of forest types (clear-cut to mature). A snag was defined as a tree (>20cm diameter at breast height) that had broken more than 2.5m from the base, but not less than 2m from the top (with no green branches). The log was the accompanying material lying on the forest floor. Trunk window traps were used to sample the fauna on both snags and logs. Decay state and amount of sun-exposure were recorded for each sample, but the age of the dead wood could not be determined.	Neither substrate type (snag or log), nor sun-exposure, affected total species abundance. However, more saproxylic species were found on snags rather than logs. One red-listed species (*Scaphisoma boreale*) was positively associated with sun-exposure. The probability of red-listed species presence was higher on snags than logs. CCA indicated that red-listed species are least likely to be found on logs with low-levels of sun-exposure. Additionally, red-listed species found in sun-exposed snag sites were both numerous and specialised while those found on shaded log sites were less abundant and less specialist.
Väisänen et al. (1993)	Finland	A saproxylic beetle assemblage 107 species (*not stated*)	Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated forests	A comparison of saproxylic beetle assemblages in managed and unmanged primeval forest areas (mean age of 250 years). The following trunk variables were measured: 1. basal diameter (cm) 2. position of the trunk (standing or fallen) 3. degree of decay (timber hard, soft or very soft) 4. Proportion of bark still attached (intact, broken or partially missing, majority missing) 5. area of bark examined (dm^2) Sampling was carried out by removing bark and dead wood from trunks and logs. 393 samples were taken, 187 from primeval forest areas (15 sites) and 206 from managed forest areas (19 sites). Sampling was carried out between May and Sep.	Number of species and individuals was higher in managed forests than primeval unmanaged forest. However the proportion of “rare” (habitat specialist) species was higher in primeval forest. The greatest number of species was associated with larger trunks in the managed forest. More species were associated with lying trunks in the primeval forest than standing trunks. There was no relationship between the number of species or individuals with tree species, degree of decay, cover and looseness of attached bark.
Wermelinger et al. (2002)	Switzerland	A saproxylic beetle assemblage	50 year old alpine spruce	An investigation of the saproxylic assemblage within three windthrow areas that were monitored for 10 years, after the	Maximum numbers of beetles were trapped in Jun/Jul each year.

	consisting of: 38 scolytid species, 37 cerambycid species, 11 buprestid species (*16 German red-listed species*)	forest	storm Vivian in 1990, and compared to an intact area of control forest. The 3 windthrow areas were subdivided into 3 pairs of plots: 1. cleared areas (timber removed and only stumps remained) 2. uncleared areas (all wood left *in situ*) areas. Samples were collected using two different trap methods (window and yellow traps) during six summer periods over the 10 years. Shannon Weaver indices were used to compare species richness across years and Sørensen's coefficient C of similarity was used to compare faunal composition of the two treatments	Beetle abundance and species richness increased over the initial 5 year period. Scolytidae numbers peaked in 1992, but declined to very low levels over the next 4 years. This peak can be attributed to the presence of the bark beetle *Ips Typographus*. Buprestidae peaked in 1994, then decreased slowly, and Cerambycidae continued to increase through time. Species richness was highest in the second year. The uncleared windthrow areas had higher beetle abundance and species richness than cleared areas. Buprestid and cerambycid species were 30-500 times more abundant in the windthrow areas than the adjacent intact control forest. The number of species present was also 2-4 times greater in the windthrow areas than in the forest. The species *Cryphalus abietis*, *Hylastes cunicularius* (scolytids), *Alosterna tabacicolor* (cerambycid) were notably more abundant in the forest. The key species in the windthrow areas were: Scolytids: *Pityogenes chalcographus*, *Crypturgus pusillus* (uncleared areas) and *Orthotomicus laricis*; Buprestids: *Anthaxia helvetica* and *Anthaxia quadripunctata*, but all the buprestids greatly preferred the windthrow habitats; Cerambycids: *Pachytodes cerambyciformes* and *Gaurotes virginea*

Appendix Three: studies comparing the effects of different types of artificial management intervention on the saproxylic assemblage

Study	Country	Taxonomic Group(s) and No. of Species (*conservation status*)	Habitat	Brief Summary of Methods	Brief Summary of Results
Alexander (1999)	England	A saproxylic invertebrate assemblage (*not stated*)	Ancient pedunculate oak (*Quercus robur*) pollards which had been enveloped within secondary woodland	A comparison of saproxylic assemblages in dead wood left in sun and shade. Two types of early successional decaying wood were placed in netting tents (Owen traps): 1. oak-branch sections (diameter 10-20cm) with bark still firmly attached, that had been cut and left following tree surgery 2-3 years previously. 2. larger items of bough (diameter >20cm) with very little or no bark attached, with well decayed heartwood following colonisation with the bracket fungus *Laetiporus sulphurous*. The open wood was gathered from 3 areas: 1. open sunshine (area of clearance and tree surgery) 2. heavy shade (area with no recent management) 3. transition zone	There was no degree of overlap in the fauna from the unshaded, shaded and transition areas for all of the “more interesting” species; each situation had its own specialist fauna, including nationally scarce species. Greatest abundance and species-richness was found in the transition zone. Branch wood in the heavily shaded area produced a more “restricted” fauna than in the open area.
Cheesman et al. (2003)	England	A saproxylic invertebrate assemblage (*not stated*)	Beech (*Fagus sylvatica*) and oak (*Quercus robur*) dominated wood-pasture.	A comparison of the saproxylic assemblage in three different types of artificially created substrate and a control: 1. re-erected bole (the upper section of an old hollow beech tree blown down in a gale, re-erected a year later and filled with a mixture of beech sawdust, chicken droppings, small animal corpses and other organic debris. Left for a further 14 years) 2. stacks (cross sections of sound beech trunk, with the core removed and filled beech sawdust and pigeon droppings. The cross sections were pilled up into stacks and left for 5 years) 3. metal dustbin (containing beech sawdust and pigeon droppings. Left for years 14 years)	Saproxylic nematodes were recovered from all substrates sampled, although they only occurred at low abundance. Nematode diversity was greatest in the stacks. The sample from the naturally hollowed ancient beech tree yielded the highest diversity of saproxylic beetles and included both generalists and specialist species associated with ancient trees.

				4. control (naturally hollowed ancient beech tree) 21g samples were taken from each substrate. A sub-sample of 25ml underwent nematological assessment. The remaining material was sieved and any entomological specimens and remains were identified.	
Fager (1968)	England	An invertebrate assemblage. The number of saproxylic species was not stated. (*not stated*)	Deciduous woodland dominated by 150 year old oak (*Quercus robur*), with ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) also present.	A control trial comparing four types of simulated log (boxes of compressed oak sawdust) and natural logs. All natural logs were <7.5cm in diameter and <70cm long (n = 15). The simulated logs were boxes 5cm square by 30cm long. The four different types were: 1. packed solid with oak dust (n = 8) 2. packed solid, but with two longitudinal boreholes (n = 8) 3. packed solid, but enriched with bone and maize flour (n = 8) 4. combination of 2 and 3 (n = 8) All logs were placed under oak trees at the edge of patches of sycamore coppice. Logs that were in the wood between May and Oct, May and March and Oct to Apr were compared.	106 species were found in both types of log (simulated and natural). The relative abundance and number of individuals per log did not significantly differ between the natural and simulated logs. Simulated logs had fewer species per log than the natural logs. The presence of boreholes had no effect on the number of individuals per log. However, there was a highly significant increase in the number of species per log. Enrichment increased both the number of individuals and the number of species in the logs. Season had no effect on the number of individuals per log, but there were significantly more species per log in those that were in the wood from May to Oct.
Hammond et al. (2001)	Canada	A saproxylic beetle assemblage 49 taxa identified to genus or species level (*not stated*)	Trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) dominated stands, which also contained white spruce (*Picea glauca*) and birch (*Betula papyrifera*)	A comparison of the saproxylic assemblages on newly created coarse woody material (CWM) of different construction. Live aspen was cut in 2 regions during spring. This was replicated in five stands of each age class: 1. old (>100 years) 2. mature (40-80 years) Three dominant aspen trees were cut in each of the 10 stands so as to leave a 120cm high stump in the ground. Two 120cm long sections were cut from the base of each felled tree; one was left on the ground as a log, and the second was suspended with a rope 1-2m above the ground to simulate a snag. Tree diameter was 24.1 to	Abundance, species richness and diversity were similar in both regions. There was no effect of stand age on mean species richness, abundance or diversity. However, the trend was for these estimates to be higher at the old stands. 28% of taxa were exclusively captured in mature stands, compared to 57% in the old stands. Neither species richness, nor catch of saproxylic beetles, was affected by wood type. However, there was a less diverse assemblage in snags than

				44.5cm (mean 33.8cm) in old stands and 15.8 to 28.6cm (mean 22.9 cm) in mature stands. Core samples were extracted at breast height from the heartwood of standing live trees to determine extent of fungal infection. The following year, 60cm long bolts were cut from each snag, log and stump and the fauna reared. Samples were reared and specimens collected between May and Oct.	either stumps or logs. 32% taxa collected from stumps, 18% beetles from logs and 25% from snags were exclusively captured in the respective CWM types
Jonsell & Weslien (2003)	Sweden	A saproxylic beetle assemblage 49 species (*2 Swedish red-list species*)	Norway spruce (*Picea abies*) dominated stand that was 90 years old.	A comparison of saproxylic beetle assemblages on: 1. standing high stumps 2. short lying boles (basal part of the tree) 3. long lying boles (from higher up the trunk of the tree). Three of each of these dead wood types were left in place after clear-cutting six plots (314m^2). One year after felling the percentage of the dead wood covered by galleries was estimated, as well as their location on the sample. Species were identified by gallery characteristics and from samples of dead wood. Three years later further sampling was carried out via sieve sampling of bark and counting rearing holes. For each species found, differences in density of individuals per m^2 of bark were compared.	6 species were found after one year (early succession species) and 43 were found after four years (late succession species that included both red-list species found in the study). The total number of species, number of species per wood unit and number of unique species were greater in boles than stumps. There were only a few minor differences between the two types of bole. Several species were largely restricted to stumps (early succession, *Hylurgops palliates*; late succession, *Hadreule elongatula*, *Ipidia binotata, Lygistopterus sanguineus*). Other species were largely restricted to boles (early succession, *Monochamus sutor*, *Pityogenes chalcographus*; late succession, *Aradus corticalis*) and three late successional species were exclusively found in boles (*Pteryx suturalis, Tyrus mucronatus, Gyrophaena boletti*). The red-listed species *Eutheia linearis* had previously only ever been associated with deciduous trees, but was found on spruce in this investigation. *Ipida binotata* is considered rare in Sweden and is not usually found in managed forests. However, it

					was abundant in the managed stand in this study.
Jonsell et al. (2004)	Sweden	A saproxylic beetle assemblage 116 species (*21 Swedish red-listed species*)	Deciduous dominated forest stands, although Norway spruce (*Picea abies*) is abundant	A comparison of saproxylic beetles assemblages on natural and man-made high stumps of aspen (*Populus tremula*) and birch (*Betula* spp) in two sites. Man-made stumps were created in 1995 using explosives placed at 5m on living trees. The influence of the following variables on the fauna was examined: 1. stump type (man-made or natural) 2. sun-exposure (shaded, semi-shaded or unshaded) 3. decay class (dead for one summer, older wood but still hard or highly decayed wood) 4. tree diameter (cm at breast height) 0.25m^2 of bark was stripped from each stump and sieved. Samples collected in Sep one year, then Oct three years later.	95 saproxylic species (including 13 red-listed species) were found on man-made stumps. 72 (10 red-listed) species were associated with aspen and 58 (5 red-listed) species were on birch. 95 species (16 red-listed) were also found on natural stumps. 62 (8 red-listed) were on aspen and 68 (10 red listed) were on birch. For similar sample sizes, natural stumps had more species and more red-listed species than man-made stumps. Trees in a later stage of decay harboured more species and more red-listed species than the newer dead wood. Species numbers were similar across all exposure and diameter categories. Tree species, stump type, decay class and stump diameter all had an influence on species composition on a stump, when investigated by CCA. However, tree species was the most important variable. Species specific habitat requirements were modelled for 28 species. All 3 red-list species (*Platysoma deplanatum, Cerylon deplanatum, Xyleborus cryptographus*) analysed in this way were associated with man-made stumps. Differences in stump type and tree species affected the presence of most species.
Lindhe & Lindelöw (2004)	Sweden	A saproxylic beetle assemblage 316 species (*40 Swedish red-listed species*)	A Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated forest, which also contained birch	The saproxylic assemblages of cut high stumps of spruce, birch, aspen and oak were monitored for 7 years following harvesting. 5 plots (50 x 100m) were surveyed in previously unmanaged secondary forest, after half of the plot was thinned and the other half was clear-cut.	Stumps of different dead wood species hosted different assemblages. However, the saproxylic fauna of the deciduous dead wood were similar. More species were found on spruce than any other species, and 48% of species found on spruce were not found on other dead wood species.

			(*Betula* spp.), aspen (*Populus tremula*) and oak (*Quercus robur*)	In each plot, and in the surrounding intact forest, Norway spruce (n = 31), birch (n = 35), aspen (n = 40) and oak (n = 24) were cut to produce 130 4m high stumps. Tree diameter and number of species of macro-fungi were recorded for each stump. Degree of sun-exposure was measured in each sub-plot via net evaporation estimates. Stumps were sampled over 7 years, between Apr and Aug, using a mix of flight barrier, intercept and emergence traps.	Aspen dead wood haboured the most red-listed species. Numbers of species and red-listed species were significantly related to increasing trunk diameter and sun-exposure.
Martikainen (2001)	Finland	A saproxylic beetle assemblage 272 species (*23 Finnish threatened species*)	Old-growth stands and clear-cut stands with aspen (*Populus tremula*) present	An investigation of the saproxylic assemblages in aspen dead wood. The following types of stand were chosen in 2 regions: 1. a one spruce dominated old-growth stand, with aspen that had died naturally. 2. a clear-cut with most aspen trees retained intact and the trees that had died naturally 3. a clear-cut with all the aspen dead, either by notching with herbicides or girdling (removing bark around trunk). 20 trees per stand were examined in one region and 10 in the second. Only snags with a diameter at breast height of >25cm, height of >2m, and a minimum distance of 20m away from the forest edge were used. Trunks were classified into 4 decay classes: 1. live, hollow trees with large holes at the basal part of the trunk 2. recently died trees, phloem fresh 3. bark partly loose, but >50% cover remaining 4. bark loose, coverage <50%. Beetles were sampled with a modified trunk-window trap, set on the south side of the trunk 1m above the ground level. Samples were taken once a month between May and Oct.	Trees killed by notching were all decay class 4. Trees killed by girdling were in decay classes 3 or 4, indicating that inducing premature death causes bark to fall off quickly. On average, sample trunks in the old-growth forest had more bark remaining. The stands significantly differed from each other with respect to the abundance of aspen, but the number of dead standing aspens was similar in all three types of stand. The number of beetles caught in each type of stand, in each region, differed considerably. The standardised (mean number of species calculated for a fixed number of individuals) number of aspen specialists, in both regions, was highest in the clear-cut stands with natural regeneration. The number in the other two types of stand was approximately equal. The number of threatened species, in both regions, was higher in the clear-cut stands than the old-growth forest. Six species (25%) of aspen specialists were found exclusively in the clear-cut stands with natural regeneration.

				Species were assigned into three groups, with some overlap: 1. aspen specialists 2. threatened species according to the Finnish Red Data book 3. uncommon species (<25 records known in Finland between 1960-1990)	DCA ordination illustrated the main gradient in the data was the clear-cut to old-growth forest. CCA identified bark cover as the most significant variable contributing to the assemblages in both regions.
Ulyshen et al. (2004)	USA	A saproxylic beetle assemblage consisting of: Buprestidae Cerambycidae Brentidae Bostrichidae Curculionidae 126 species (*not stated*)	Hardwood forest (75 years old) dominated by bald cypress (*Taxodium distichum*) and oak (*Quercus spp*.)	A comparison of saproxylic beetle abundance and diversity in artificially created canopy gaps of varying size: 1. 0.13ha 2. 0.26ha 3. 0.50ha For each size class there were 4 gaps that had been created 7 years previously and 4 gaps that had been created 1 year previously. Malaise traps were used to sample the beetle fauna in the gap centre, gap edge and 50m into the surrounding forest. Samples were collected between May and Nov.	Abundance and diversity of saproxylic beetles was higher in younger gaps than in older gaps. Abundance was higher in the centre of young gaps, compared to in the surrounding forest. For old gaps, the surrounding forest and gap-edge had higher abundances and diversity of saproxylic beetles than the centre of the gap. Gap size had no significant effect on beetle abundance, but diversity was lower in 0.13 ha gaps.
Wilkars et al. (2005)	Sweden	A saproxylic beetle assemblage 185 species (*13 red-listed species)*	A managed forest comprising of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)	A comparison of saproxylic beetle assemblages in three different types of dead wood: 1. sun-exposed logs (on stand edges between mature and clear-cut areas) 2. shaded logs (mature forest ~100 years old) 3. high stumps (artificially created in clear-cut areas between 3-10 years old) Five samples of each different type of dead wood were taken at two study sites, from trees had been dead for 3-10 years. For each tree, the following measurements were taken: 1. length of dead wood 2. trunk diameter (in cm, at a height of 1.3m) 3. decomposition stage (based on hardness of the wood and mean knife penetration depth)	Species richness was higher in logs (both shaded and sun-exposed) than in high stumps. High stumps were preferred by some red-listed species, but red-listed species were found on all three types of dead wood.

			Beetles were sampled using window traps, emergence traps and sieving $0.5m^2$ of bark between May and Oct.