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ORIGINAL PAPER

Are current management recommendations for saproxylic invertebrates effective? A systematic review

Zoe G. Davies · Claire Tyler · Gavin B. Stewart · Andrew S. Pullin

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Abstract Conservation management recommendations for saproxylic invertebrates advocate the continuous provision of the dead and decaying wood microhabitats that they require for survival. Accepted site-based management practices include leaving fallen dead and decaying wood in situ, 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. Here we examine the empirical evidence regarding the effectiveness of such interventions using rigorous systematic review methodology. Systematic searching yielded 27 studies containing pertinent information. The evidence presently available is insufficient to critically appraise the utility of any specific intervention for conserving saproxylic species, or assemblages, in the long-term. However, there are a range of studies, conducted over relatively short periods of time, which do describe changes in saproxylic fauna in response to management practices. In the absence of robust, high quality evidence, recommendations relating to the use of specific site-based conservation interventions should only be regarded as speculative. Nonetheless, 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 be encouraged even though experimentally controlled and replicated evidence is lacking. Further primary research and long-term monitoring are required to fill the gaps in our ecological knowledge that potentially weaken the case for the effectiveness of current

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Z. G. Davies · C. Tyler · G. B. Stewart · A. S. Pullin (✉)
Centre for Evidence-based Conservation, School of Biosciences, University of Birmingham,
Edgbaston, Birmingham B15 2TT, UK
e-mail: a.s.pullin@bangor.ac.uk

Z. G. Davies
Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of
Sheffield, Sheffield S10 2TN, UK
e-mail: z.davies@sheffield.ac.uk

Present Address:
G. B. Stewart · A. S. Pullin
Centre for Evidence-based Conservation, School of the Environment and Natural Resources,
University of Wales Bangor, Bangor, Gwynedd LL57 2UW, UK

saproxylic invertebrate conservation action and would enable practitioners to make better informed decisions with regard to dead wood protection and provision.

Keywords Coarse woody material (CWM) · Coleoptera · Conservation · Dead wood · Decaying wood · Diptera · Forestry · Microhabitat · Old-growth · Veteran trees

Abbreviation

CWM	Coarse woody material

Introduction

Throughout Europe, saproxylic insects have been identified as a highly threatened taxonomic group (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 in Finland are categorised as threatened (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 have dramatically modified the biotic and abiotic processes occurring within forest and woodland ecosystems. In other parts of the world, particularly in tropical regions, the status of many saproxylic species remains undocumented and their habitat associations yet to be characterised (Grove 2002a). However, the threats faced by the saproxylic fauna in these areas are likely to be equally significant as those in Europe (Ghazoul and Hill 1999).

'Saproxylic' invertebrates are obligate on microhabitats associated with the processes of decay and damage in the bark and wood of trees, large woody scrub and climbers (Speight 1989; Fowles et al. 1999). The saproxylic fauna is responsible for the mechanical breakdown of woody material (Cavalli and Mason 2003) both directly, by tunnelling and feeding in living trees that are decaying, snags (standing dead trees) and logs (fallen trees, portions of trunk and large branches), or indirectly, through symbiotic relationships with fungi and other micro-organisms that humify wood (Speight 1989). Decaying wood and saproxylic invertebrates contribute to a number of terrestrial ecosystem functions 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 and Mason 2003). The presence of dead wood and saproxylic species, particularly beetles (Coleoptera), in forests, woodlands, parklands or open pasture-woodland is indicative of 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 and Wilde 2003; Alexander 2004).

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 and Walheim 2000; Grove 2001a; Larsson and Danell 2001; Siitonen 2001). For example, in commercial forestry, dead and decaying wood is 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 and Väisänen 1984; Mikkola 1991; Warren and Key 1991; Wilson 1992; Väisänen et al. 1993; Haila et al.

1994; Kaila et al. 1994; Siitonen and Martikainen 1994; Kouki et al. 2001). One such region 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 and Rose 1986; Stubbs and Falk 1987; Speight 1989; Alexander 1996, 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 and Crawley 1994; Nilsson 1997; Kirby and Watkins 1998; Read 2000). A strong positive correlation has been demonstrated between tree age and high saproxylic species richness (Rose 1976; Harding and Rose 1986; Rackham 1986; Speight 1989; Harding and Alexander 1994).

The decline in saproxylic species diversity has only been widely acknowledged in the last few decades (Esseen et al. 1992, 1997; Alexander 1998; Grove 2002a). 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 and Elbourn 1993; Cheesman and 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 North America, Australia and many European countries (Grove 2001b; Butler et al. 2002; Grove 2002a). The preservation and continuity of veteran trees has also become a high conservation priority in recent years (Speight 1989; Harding and Alexander 1993, 1994; Nilsson and Baranowski 1994; Fowles et al. 1999). In Britain, for example, ecological groups including the Ancient Tree Forum (ATF) and the Veteran Tree Initiative (VTI) have done much to endorse their conservation. In turn, this has promoted the maintenance and provision of suitable habitat for the saproxylic invertebrate fauna (Read 2000; Alexander 2004).

Site-based conservation management recommendations for saproxylic invertebrates advocate the continuous provision of dead and decaying wood (e.g., Kirby and Drake 1993; Alexander et al. 1996; Kirby 2001; Cavalli and Mason 2003). It is suggested that this can be achieved by protecting veteran trees, leaving dead or decaying wood in situ, 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 and Lonsdale 1991).

In this paper, we report on the process and outcome of a systematic review of available empirical evidence relating to the question ‘Are current management recommendations for conserving saproxylic invertebrates effective?’. The rationale for undertaking the review was to evaluate the utility and success of site-based interventions in order to allow practitioners to make better informed decisions with regard to the provision of dead and decaying wood. 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.

Methods

Systematic review is a technique used to locate information from published and unpublished sources, critically appraise methodology and synthesise evidence in order to answer a question concerning the effectiveness or impact of an intervention. Systematic reviews differ from conventional literature reviews as they follow a strict methodological protocol and provide a comprehensive assessment of all available empirical evidence (Khan et al. 2003). They are therefore extensive, repeatable and minimise the chance of incorporating bias into the review process, whereas a conventional review may reflect the personal view of author(s) and may be based on a (potentially biased) selection of literature (Roberts et al. 2006). The use and value of systematic review and the evidence-based approach is well established in the medical and public health sectors (Stevens and Milne 1997; Egger et al. 2003), and is now widely recognised in other research disciplines, including conservation and environmental management (Pullin and Knight 2001; Sutherland et al. 2004; Pullin and Stewart 2006; further details of the methodology and completed systematic reviews can be found at http://www.cebc.bangor.ac.uk).

Question formulation

A systematic review is a project undertaken by independent academic researchers, but also involves close collaboration with practitioners, policy makers and additional interested stakeholder groups. In this instance, The National Trust (a substantial private charity that owns and manages land throughout England, Wales and Northern Ireland for conservation objectives) identified the need for a systematic review to evaluate the effectiveness of site-based management interventions for conserving saproxylic invertebrates. The specific nature of the question to be addressed was formulated via iterative discussion between UK-based governmental and non-governmental conservation 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 the proposed methodological protocol, prior to finalisation and initiating the research. The question was constructed of three key elements (Pullin and Stewart 2006):

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 (i.e., the measured result from a study on the effectiveness of the intervention): the desired 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.

Identification of relevant studies

Relevant studies were identified through computerised searches of the following electronic databases: ISI Web of Knowledge (comprising of ISI Web of Science: Science Citation

Index Expanded 1945-present and ISI Proceedings: Science and Technology Proceedings 1990-present), JSTOR, Science Direct, Directory of Open Access Journals (DOAJ), Copac, Scirus, Scopus (1960–2005), Index to Theses Online (1970–2005), Digital Dissertations Online, Agricola, CAB Abstracts, English Nature's 'WildLink' and Countryside Council of Wales (CCW) library (providing access to grey literature of relevance to EN and CCW, the English and Welsh governmental conservation agencies, respectively). Couplets of key words were used for searching, consisting of 'invertebrate' combined with the following: fallen wood, dead wood, over-mature tree, pollard, brash and conservation (wildcards were used where supported by the database). In addition, the more specific terms 'saproxylic', 'Coleoptera and conservation' and 'Diptera and conservation' were used.

Publication searches were also conducted via the internet meta-search engines Alltheweb and Google Scholar, with the first 50 word document or PDF hits from each website being examined for appropriate literature or data. The following statutory and non-governmental 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). Additionally, the specialist publication 'Coleopterist' was searched by hand for any appropriate information. Bibliographies of articles accepted into the full text stage of the systematic review and conventional literature reviews were both searched for studies that had not yet been identified by any other means. Finally, recognised experts and practitioners were contacted and asked to recommend any additional sources of potentially relevant information.

Non English language searches were not conducted in this systematic review. However, the search did identify research conducted in North America, Australia and Europe and all suitable studies were included into the start of the systematic review process irrespective of geographic location.

Studies underwent a three-fold filter process before being accepted into the final systematic review. Initially, all articles were filtered by title and any obviously irrelevant material was removed from the list of captured articles. Subsequently, the abstracts of the remaining studies were examined, by two independent reviewers, with regard to possible relevance to the systematic review question, using inclusion criteria based on the subject and intervention elements of the systematic review question. No study was rejected due to the outcome measure (i.e., regardless of whether it recorded change in species diversity or species abundance, etc.). Articles 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. Finally, all remaining studies were read at full text and either rejected or accepted into the final review.

Data extraction and analysis

Information relating to each of the systematic review question elements was extracted from the studies and collated in qualitative tables. The broad variation in type of investigation conducted and the range of outcome measures adopted in the studies precluded the use of formal meta-analytical techniques for quantitative analysis. Direct comparisons between studies of saproxylic invertebrate species must be made with extreme 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. Nevertheless, 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).

Results

Search statistics

Searching was completed in October 2005. From over 6800 initial hits (including duplicates) from all searches, 286 unique studies remained in the systematic review after the abstract filter stage. However, 32 of these 286 studies could not be obtained at full text for further examination as they were unavailable from the British Library, author(s) or publishers. Following assessment at full text, the final review incorporated 27 studies.

Review outcome

None of the studies examined at full text report changes in the long-term persistence of saproxylic invertebrate populations, or increased species richness within assemblages, as a direct result of a specific site-based intervention. 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 high quality evidence is lacking, there are studies that provide relevant information on the influence of various habitat management actions on the saproxylic fauna in the short-term.

The 27 studies were divided into two groups. The first (Table 1) consisted of studies that investigated the saproxylic invertebrates in managed (e.g., clear-cut or thinned) and unmanaged sites (e.g., mature or old-growth forest). The second group (Table 2) 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 majority of studies focused on saproxylic beetles, although other taxonomic groups were represented.

Saproxylic invertebrates in managed and unmanaged wooded habitats

The results of many of the studies were contradictory. For example, Martikainen et al. (2000) and Sippola et al. (2002) recorded a greater number 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 were also apparent for investigations into the distribution of species within the CWM on sites; Sverdrup-Thygeson and 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 patterns were 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; Grove 2002b; Similä et al. 2002a; Sippola et al. 2002; Similä et al. 2003). In addition, managed and unmanaged

Table 1 A summary of the characteristics and results of studies investigating saproxylic invertebrates in managed and unmanaged wooded habitats

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Grove (2002b)	Australia	Saproxylic Coleopteran assemblage 118 species (*not stated*)	Lowland tropical mesophyll vine rainforest, dominated by evergreen trees	Old-growth, logged and re-growth (30–90 years old) forest (*1 field season*)	Species richness and abundance in old-growth areas were significantly higher than in re-growth sites. Species abundance was higher in old-growth sites than in logged sites. Only two species were more abundant in re-growth sites than in old-growth areas, and one species (*Mimemodes laticeps*) in re-growth rather than logged sites. One species (*Eutinophaea variegata*) was more abundant in logged sites than either re-growth or old-growth areas
Hammond et al. (2004)	Canada	Saproxylic Coleopteran assemblage 257 taxa, mostly identified to species level (*not stated*)	Trembling aspen (*Populus tremuloides*) dominated stands, also containing balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*) and birch (*Betula papyrifera*)	Logs and snags in old (>100 years old) and mature (60–90 years old) stands (*2 field seasons*)	CWM from old stands had 34% more species and twice the no. of individuals than that from mature areas, but relative species richness did not differ between the two stands. Of the 257 taxa collected, 54 ‘rare’ species (<10 specimens each) were collected exclusively from old stands. Forty four species were only found in mature stands. Beetle assemblages on logs and snags were 60% similar. Forty seven species were unique to either logs or snags. Higher no. of individuals were found on less decayed CWM, but species diversity was lower that in highly decayed CWM. The no. of ‘rare’ species increased with increasing snag diameter

Table 1 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Kaila et al. (1997)	Finland	Saproxylic Coleopteran assemblage 129 species (*not stated*)	Two mixed forests of birch, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), between 70–80 years old, with a tree canopy cover of 70–85%	Dead white-rotted birch trunks in mature and recently clear-cut (<5 years ago) areas, and before and after clear-cutting (3 years) (*1 field season*)	Clearest variation in the assemblage was between mature and clear-cut areas; both types of forest harboured different beetle faunas. There was no difference in the no. of beetles in the clear-cut and mature forest areas. Significantly more species, but lower no. of individuals, were found in the managed area after the clear-cut. The no. of species remained the same in the mature area, before and after clear-cutting. Rare species were recorded in the clear-cuts and *Denticollis borealis* was only found in these areas. The threatened species *Triplax rufipes* and *Carphacis striatus* were only found in mature forest
Lindhe and Lindelöw (2004)	Sweden	Saproxylic Coleopteran assemblage 316 species (*40 Swedish red-listed species*)	Norway spruce and Scots pine dominated forest, also containing birch (*Betula* spp.), aspen and oak (*Quercus* spp.)	High stumps of spruce, birch, aspen and oak in unmanged, thinned and clear-cut forest (*7 field seasons*)	High stumps of different tree species harboured different assemblages, although the fauna of the deciduous high stumps was similar. The greatest no. of beetles was found on spruce and 48% of these were not found on any other tree species. Aspen high stumps had the most red-listed species. The no. of species and red-list species were significantly related to increasing trunk diameter and sun exposure
Martikainen et al. (2000)	Finland	Coleopteran assemblage 553 species in total 232 saproxylic species (*not stated*)	Norway spruce and Scots pine dominated forests	Mature (95–120 years old, cut stumps abundant), over-mature (>120 years old, cut stumps abundant) and old-growth (>160 years old, no or few cut stumps present) forest (*1 field season*)	Saproxylic species richness and abundance was significantly higher in old-growth forests than in managed forests. The species assemblages in the different types of forests had limited overlap. The total no. of saproxylic species were positively correlated to 90% of measured dead wood characteristics. The strongest relationship was with the total volume of dead wood (highly intercorrelated with other ecological variables)

Table 1 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Moretti et al. (2004)	Switzerland	Arthropod assemblage, including the following saproxylic Coleopteran families: Cerambycidae Buprestidae Lucanidae (*not stated*)	Alpine forest	Different intensity of forest fires (burnt once, 3–4 burns and unburnt in 30 years) (*1 field season*)	Tree canopies were more open, grass cover was greater and the diameter of dominant trees was smaller on sites that had been burnt. Fire had a positive, but not significant, effect on species richness within saproxylic families. *Chlorophorous figuratus* and *Stenopterus rufus* were only found in sites that had been burnt
Økland et al. (1996)	Norway	Saproxylic Coleopteran assemblage 194 species (*21 Norwegian red-listed species*)	Norway spruce dominated forest (>80 years old)	Spatial scales (small, medium and large plots of 0.16 ha, 0.32–0.48 ha and 4 km^2, respectively) in mature forest (*1 field season*)	Dead wood and wood inhabiting fungi related variables had a significant positive effect on species richness across all spatial scales (many of the variables were highly intercorrelated). Level of disturbance, landscape ecology and surrounding vegetation structure did not influence species richness. Former clear-cutting only had a negative effect on species richness at a large spatial scale
Ranius and Jansson (2000)	Sweden	Saproxylic Coleopteran assemblage 120 species (*48 Swedish red-listed species*)	Oak (*Quercus robur*) dominated forest	Living hollow oak trees in mature forest plots (*1 field season*)	Species richness was greatest in plots with large, free standing trees. Wide girth and low canopy cover increased the frequency of occurrence of several species. Forest re-growth was detrimental for many species. There was no difference in the occurrence of species and red-listed species

Table 1 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Ranius (2002)	Sweden	Saproxylic Coleopteran assemblage 47 species (*20 Swedish red-listed species*)	Oak dominated forest	Living hollow oak trees in mature forest plots (*1 field season*)	Species abundance was higher in larger trunks, but this was only significant for *Tenebrio opacus* and *Procraerus tibialis*. No species showed a preference for shaded or unshaded trees. Most species were absent from hollows with an entrance directed upwards. Species richness was greater in hollows situated higher up the tree. Species richness per tree increased in larger stands
Schiegg (2001)	Switzerland	Saproxylic assemblage 426 Diptera 228 Coleoptera (*66 Swiss red-listed Coleopteran species*)	Beech and Norway spruce dominated forest, also containing ash (*Fraxinus excelsior*) and fir (*Abies alba*) trees	Beech trunks and limbs (*1 field season*)	Limbs harboured more species and had a higher diversity than trunks for both taxonomic groups. Sixty beetle species collected from the trunks and 66 species collected from the limbs were red-listed. About 82.6% of beetles and 55.3% of flies were present in both trunks and limbs
Siitonnen and Saaristo (2000)	Finland	Saproxylic Coleopteran species *Pytho kolwensis* (*on the Finnish and Swedish red-list*)	Norway spruce dominated forest, also containing Scots pine, birch (*Betula* spp.) and aspen (*Populus tremula*)	Spruce trunks in different areas (*1 field season*)	Thirty eight percent of sampled host trees were inhabited by *P. kolwensis*. Eighty seven percent of trees hosting *P. kolwensis* had a trunk diameter of >20 cm, >50% bark cover, >1.5 cm 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 (73–111 $m^3 ha^{-1}$) present

Table 1 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Similä et al. (2002a)	Finland	Coleopteran assemblage No. of saproxylic species was not stated (*12 Finnish red-listed saproxylic species*)	Scots pine dominated forest	Successional stages (<7, 40, 70, 110, >150 years old for sapling, young, middle-aged, mature and old-growth stands, respectively) in managed and semi-natural forest (*1 field season*)	Semi-natural and managed forests contained different assemblages. The earliest stage successional areas harboured a different assemblage to the later successional areas. The no. of rare saproxylic species was higher in semi-natural forests than managed forests, although this trend was not statistically significant
Similä et al. (2003)	Finland	Saproxylic Coleopteran assemblage 186 species (*33 Finnish red-listed species*)	Scots pine dominated forest	Successional stages (40, 70, 110, >150 years old for young, middle-aged, mature and old-growth stands, respectively) in managed and semi-natural forest (*1 field season*)	Fifty two percent of species were common to both forest types, 21% restricted to managed stands and 27% restricted to semi-natural stands. Bark beetles were more abundant and diverse in semi-natural forests, although this was not statistically significant. Bark beetle species richness was positively related to volume and diversity of dead wood. Assemblages of other beetles were different between semi-natural and managed forests. Diversity and volume of dead wood were positively correlated with species richness in managed areas only. Red-list species richness was greatest in semi-natural forests and positively correlated with volume of decayed wood and diversity of dead wood
Sippola et al. (2002)	Finland	Saproxylic Coleopteran assemblage 180 species (*2 Finnish red-list species, 29 nationally rare species*)	Norway spruce and Scots pine dominated forest	Old-growth (areas dominated by pine, spruce and spruce with some deciduous trees) with managed (1 year old seed-tree cut pine, 15 year old seed-tree cut pine and 15 year clear-cut spruce) forests (*1 field season*)	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, or between any of the cutting treatments. More rare saproxylic species were found in old-growth forest than in managed forests. Species richness correlated positively with measures of dead wood availability and site fertility (volume of living trees and % cover of eutrophic plants)

Table 1 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Comparison (*duration of investigation*)	Key results
Sverdrup-Thygeson and Ims (2002)	Norway	Saproxylic Coleopteran assemblage 232 species (*18 Norwegian red-listed species*)	Norway spruce and Scots pine dominated forest, also containing birch (*Betula* spp.) and aspen	Aspen snags and logs (*2 field seasons*)	Total species abundance was not affected by either type of CWM or the degree of sun exposure. One red-listed species (*Scaphisoma boreale*) was positively associated with sun-exposure. More species were found on snags than logs. The probability of red-listed species presence was higher on snags than logs. Red-list species found in sun exposed snag sites were both numerous and specialised, whereas those found on shaded log sites were less abundant and less specialist
Väisänen et al. (1993)	Finland	Saproxylic Coleopteran assemblage 107 species (*not stated*)	Norway spruce and Scots pine dominated forest	Unmanaged primeval (250 years old) and mature managed forest (*1 field season*)	The no. of species and individuals were higher in managed forests than primeval unmanaged forest, but the proportion of 'rare' habitat specialist species were higher in primeval forest. The greatest no. of species was associated with larger trunks in the managed forest. More species were associated with fallen trunks than standing trunks in the primeval forest. There was no relationship between the no. of species or individuals with tree species, degree of decay, cover and looseness of attached bark
Wermelinger et al. (2002)	Switzerland	Saproxylic Coleopteran assemblage 38 scolytid species, 37 cerambycid species 11 buprestid species (*16 German red-listed species*)	50 year old alpine spruce forest	Cleared and uncleared windthrow areas caused by a storm and an intact control area of forest (*6 field seasons in 10 years*)	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. Buprestidae peaked in 1994, then decreased slowly, and Cerambycidae continued to increase through time. Species richness was highest in the second year. 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 control forest

Table 2 A summary of the characteristics and results of studies examining the impact of specific management interventions on saproxylic invertebrates

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Intervention (*duration of investigation*)	Key results
Alexander (1999)	England	Saproxylic invertebrate assemblage (*not stated*)	Ancient oak pollards, enveloped within secondary woodland	Two to three year old sections of oak branch wood and well decayed sections of bough in full sun, heavy shade and a transition area (*1 field season*)	CWM from each location had its own specialist fauna, including nationally scarce species. Heavily shaded CWM had a restricted assemblage. Transition zone had the greatest abundance and species richness
Cheesman et al. (2003)	England	Saproxylic invertebrate assemblage (*not stated*)	Beech and oak dominated wood-pasture	Hollowed ancient beech tree (control) and three simulated hollow trees: re-erected bole (*14 years old*), stacks (*5 years old*) and metal dusbin (*14 years old*) (*1 field season*)	All types of CWM had a low nematode abundance. Nematode diversity was greatest in the stacks. The control had the greatest beetle diversity and included both generalists and specialist species associated with ancient trees
Fager (1968)	England	Invertebrate assemblage No. of saproxylic species not stated (*not stated*)	Deciduous woodland dominated by ancient oak, also containing ash and sycamore (*Acer pseudoplatanus*)	Natural logs and four types of simulated log: oak sawdust packed, packed with boreholes, packed and enriched, packed with boreholes and enriched (*2 field seasons*)	Relative abundance and no. of individuals per log did not significantly differ between the natural and simulated logs. Natural logs had the greatest species diversity. Simulated logs with boreholes had significantly more of species than those without. Enrichment increased the no. of individuals and species in the artificial logs

Table 2 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Intervention (*duration of investigation*)	Key results
Hammond et al. (2001)	Canada	Saproxylic Coleopteran assemblage 49 taxa identified to genus or species level (*not stated*)	Trembling aspen and balsam poplar dominated stands, also containing white spruce and birch	Old (>100 years) and mature (40–80 years old) aspen trees cut to make threes types of CWM (1 year old): high stumps, logs and simulated snags (*1 field season*)	Stand age had no significant effect on mean species richness, abundance or diversity. Twenty eight percent of beetles were only found in mature aspen, compared to 57% in the old aspen. There was no significant difference in species richness or no. of beetles in the different CWM. However, there was a less diverse assemblage in snags than either the stumps or logs. Thirty two, 18 and 25% of beetles were unique to stumps, logs or snags, respectively
Hövemeyer and Schaermann (2003)	Germany	Dipteran assemblage No. of saproxylic species not stated (*not stated*)	Beech (*Fagus sylvatica*) dominated forest	Logs (2 years old) cut from 2 felled beech trees (*10 field seasons*)	Abundance of saproxylic species was positively correlated with increasing water content of the branch wood
Jonsell and Weslien (2003)	Sweden	Saproxylic Coleopteran assemblage 49 species (*2 Swedish red-list species*)	Norway spruce dominated forest	Mature (90 years old) stand clear-cut and three types of CWM left in place: high stumps, short and long lying boles (4 years old) (*1 field season*)	Six species were found after 1 year and 43 after 4 years. Total no. of beetles and no. of unique species were higher in boles than stumps. There were no significant differences in the assemblage between the two types of bole. High stumps and boles both had their own specialist fauna. *Eutheia linearis*, a red-list species previously only recorded on deciduous trees, was found on spruce. *Ipida binotata*, a rare species in Sweden was unusually abundant in the managed stand in this study
Jonsell et al. (2004)	Sweden	Saproxylic Coleopteran assemblage 116 species (*21 Swedish red-listed species*)	Deciduous dominated forest stands, also containing Norway spruce	Natural and man-made high stumps of aspen and birch (4 years old) (*1 field season*)	Natural high stumps had more beetles and red-listed species than man-made stumps. Highly decayed high stumps had more species and red-listed species than less rotten stumps. Tree species, type of stump, decay class and stump diameter all influenced assemblage composition, but tree species was the most important variable

Table 2 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Intervention (*duration of investigation*)	Key results
Martikainen (2001)	Finland	Saproxylic Coleopteran assemblage 272 species (*23 Finnish threatened species*)	Old-growth stands and clear-cut stands with aspen present	Aspen snags in three types of stand: spruce dominated old-growth where aspen had died naturally, clear-cut where aspen had died naturally and clear-cut where aspen was killed using herbicides or girdling (removing bark around the trunk) (*1 field season*)	Inducing premature death caused bark to fall off quicker than if left to die naturally. The no. of beetles caught in each type of stand was significantly different. The relative mean no. of aspen specialists was highest in the clear-cut stands with aspen that had died naturally and approximately equal in the other stands. Six species (25%) of aspen specialists were found exclusively in the clear-cut stands with natural regeneration. The no. of threatened species was greater in the clear-cut stands than in the old-growth forest
Ulyshen et al. (2004)	USA	Saproxylic Coleopteran assemblage 126 species (*not stated*)	Hardwood forest (75 years old) dominated by bald cypress (*Taxodium distichum*) and oak	Artificially created canopy gaps of varying size: small (0.13 ha), medium (0.26 ha) and large (0.50 ha). For each size class there were four gaps that had been created 7 years previously and four gaps that had been created 1 year previously (*1 field season*)	Abundance and diversity of beetles were higher in younger gaps than in older gaps. Abundance was also greater in the centre of young gaps compared to within the surrounding forest. In older gaps, the abundance and diversity of beetles were higher in the surrounding forest and at the gap-edge, than in the centre of the gap. Gap size had no significant effect on beetle abundance, but diversity was lower in the smallest sized gaps

Table 2 continued

Study	Country	Taxonomic group(s) and number of species (*conservation status*)	Habitat	Intervention (*duration of investigation*)	Key results
Wikars et al. (2005)	Sweden	Saproxylic Coleopteran assemblage 185 species (*13 red-listed species)*	Norway spruce and Scots pine dominated forest	Three types of CWM (3–10 years old): high stumps in clear-cut areas, sun-exposed logs and shaded logs within mature (100 years old) forest (*1 field season*)	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 CWM

wooded habitats support different saproxylic assemblages, some species of which are threatened specialists found exclusively within each respective type of site (Kaila et al. 1997; Martikainen et al. 2000; Grove 2002b; Similä et al. 2002a; Similä et al. 2003; Hammond et al. 2004).

Impact of specific management interventions on saproxylic invertebrates

A smaller number of studies (10 of the 27 in total) 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 upon 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 (Fager 1968). Although the number of species per simulated log was lower than in the natural logs, 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).

Discussion

The objective of this systematic review was to collate and synthesise published and unpublished evidence in order to critically appraise the utility and success of current management recommendations for conserving saproxylic invertebrates. Unfortunately, insufficient robust, high quality data, from long-term fully replicated and controlled field-based investigations, was found to definitively assess the effectiveness of site-based conservation interventions for a particular saproxylic species or community. None of the studies demonstrate a positive, or a negative, effect on long-term population persistence or species richness within an assemblage, as a direct result of a specific management action. However, there is some evidence describing changes in the saproxylic fauna in response to a range of management practices, observed over relatively short periods of time. The research suggests that employing a variety of different management interventions will maximise microhabitat heterogeneity and, therefore, the diversity of species present on a site. Consequently, we cannot reject the hypothesis that the long-term stability and preservation of saproxylic invertebrates can be facilitated by incorporating interventions, such as the provision of supplementary CWM, 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 if 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?). The main value of this systematic review has been to highlight that 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 projects 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, 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; Hammond et al. 2004). 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, pers. comm.).

Implications for management

Promoting the value of veteran trees and old-growth wooded habitats

In recent years, there have been considerable advances in our ecological understanding of the saproxylic 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 and act as refugia for specialist saproxylic invertebrates confined to stable old-growth decay microhabitats (Read 2000; Alexander 2004). This conclusion, although not the focus of this review, was apparent in its findings, with high numbers of rare specialist species being consistently recorded within unmanaged old-growth sites (Väisänen et al. 1993; Similä et al. 2002a, 2003; Sippola et al. 2002).

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 and Alexander 1993, 1994; Nilsson and 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 and Alexander 1993; Fowles et al. 1999; Alexander 2004).

Encouraging microhabitat heterogeneity

Ordinarily, there are numerous specialist niches along environmental gradients for saproxylic species to exploit and many species are adapted to survive in a specific successional stage 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 and Mason 2003). Habitats, such as forests, woodland and parkland, should therefore be adequately endowed with both a spatial and temporal continuity of dead and decaying wood, including veteran trees and an assorted 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 and Lonsdale 1991; Alexander 1993, 2004; Kirby 2001; Cavalli and Mason 2003).

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 and 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.

Significance for best practice for forest management

There is a deep rooted aversion towards dead wood among 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 (Grove 2002a; Cavalli and Mason 2003; Gibb et al. 2005). 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; Cavalli and Mason 2003). 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 restricted available evidence obtained in this systematic review verified that managed (e.g., clear-cut or thinned) sites, where CWM, dead and decaying trees were retained, harboured a different saproxylic assemblage to that found 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 of trees of varying age in order to reduce the uniformity of the stand (Linder and Östlund 1992; Haila et al. 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 and Väisänen 1984; Speight 1989, Martikainen 2001), they can serve as useful indicators of forest sustainability and ecosystem recovery.

Implications for research

The majority of the studies accepted into this systematic review have been conducted in forest environments in Fennoscandia. Of particular concern is the paucity of research outside of Europe and North America; only one of the accepted studies was conducted in the tropics (Grove 2002b). The saproxylic invertebrate fauna in tropical regions is likely to be highly species rich, yet appropriate management guidelines on the preservation of dead and decaying wood in such areas is frequently lacking (Grove 2001b).

Similarly, despite the widely acknowledged importance of historic parklands and open pasture-woodland in Britain, very few experimentally rigorous investigations 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. Robust primary research 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 examining 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, 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 and Lindhe 1992; Cavalli and Mason 2003; Cheesman and 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 three 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. Gibb et al. (2006a) have recently initiated one such long-term research project, which proposes to examine the conservation value of CWM throughout its lifetime.

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 and Elbourn 1993; Fowles et al. 1999; Rotheray et al. 2001; Grove 2002a; Cheesman and 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 in Europe 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 and 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; Gibb et al. 2006b). Historically, the range of many 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 and 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 and Ball 1993; Alexander et al. 1996; Schiegg 2000; Butler et al. 2002; Cavalli and 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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