A RESEARCH AGENDA FOR INSECTS AND DEAD WOOD

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Abstract—In recent years, great advances have been made in our knowledge of the ecology, evolutionary biology, biogeography and management of saproxylic insects and their dead wood habitat. There is now a greater level of awareness of the need to cater to their requirements in today's managed forest landscapes. However, having raised the profile of saproxylic insects, researchers are now being called upon to translate knowledge gains into management principles. This throws up new research challenges, many of which can only be addressed through adaptive management. This paper outlines and prioritises some of those challenges.

INTRODUCTION

This paper is unabashedly focused on a research agenda that may aid the conservation of saproxylic insects and their habitat. Whilst the focus is on terrestrial systems, it is recognised that aquatic systems deserve a similar level of attention; this paper makes occasional specific reference to aquatic systems but many of the broader principles will apply equally to terrestrial and aquatic systems. Research on 'pest' aspects of saproxylic insects is beyond the scope of this paper.

THE RESEARCH CONTEXT

No single research agenda would be appropriate for every single region because, around the world, there are great differences in the ecology and management of forests. These differences in turn influence the ecologies and the functional integrity of saproxylic insects (Grove 2002a). Two prominent influences act more or less orthogonally: (a) the natural disturbance regime to which the forests are historically adapted; and (b) the relative dominance of natural versus human-induced ecological processes. Further aspects for consideration are the historical and present level of ecological understanding of these forests and their saproxylic insect biodiversity; and the extent to which there is, or would be, opportunity to use this understanding to influence management.

In deciding priorities for a particular region, the following issues require consideration:

- Natural disturbance dynamics—What are the forest's natural disturbance dynamics? Have they evolved to cope with occasional wildfires, cyclones or pest outbreaks that can re-set the successional clock for entire forest stands? Or are they in a more or less steady state, where normal disturbance constitutes individual trees falling (e.g., as a result of windthrow, lightning, disease or old age) followed by successional infilling of the gaps created? More likely, are they somewhere in between these two extremes, e.g., occasional rare major disturbances, interspersed with more frequent smaller disturbances, resulting in a mosaic of age-classes? To what extent are current patterns of dead wood distribution and abundance in equilibrium with the current stand structure?
- Biogeography—To what extent can the forest be considered a single biogeographical unit? Is it naturally fragmented, or are there (or have there been) other internal obstacles to continuous occupation by some species, such as faunal breaks (Mesibov 1994), resulting in substantial natural turnover of species from one part of the forest to another? Is the origin of the entire forest so recent that one area would naturally support much the same set of species as any other?
- Management history—To what extent has human management altered the forest's ecological integrity, in terms of its ability to continue to respond to natural processes at ecologically relevant spatial and temporal scales? Ecologically, how far removed is the current forest from its natural predecessor? Is it fragmented, to the extent that its natural functioning is hindered? Is it in a state of transition from a 'natural' to an 'anthropogenic' forest? Has human intervention been so consistent, and/or been going on for so long, that the forest's ecology has been remoulded, with surviving biodiversity now dependent on human management? Or is it no longer possible to say what a pre-human forest would have looked like? To what extent has management affected the dead wood resource and its saproxylic fauna?
- Level of ecological understanding of forests and their saproxylic insects—How well can we already answer the above questions? How important is it, for management purposes, to know what species live in the forest and what they do? Is it more important to have the tools to be able to 'scale up', i.e., to address 'whole-of-landscape' management issues? In which case, do we understand enough about the natural and historical processes shaping our forests and their biodiversity to be able to make management recommendations? How desirable or realistic is it to seek to maintain—or recreate—conditions necessary for the survival of a saproxylic insect fauna typical of a truly natural (pre-human?) forest, versus one that is robust in response to further natural or human-induced change?
- The opportunity for scientific input into land management—If we don't know the answers to the above questions, how much difference would it make to our management if we were to do the research to find out? Is further research just an excuse for delaying management? Will anybody take

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notice of our findings? Is the purpose of continued research more to maintain or raise awareness of the issue so saproxylic insect conservation creeps higher up the political agenda? Do our institutions have the capacity to do the research, and do our management agencies have the capacity to heed its findings, given the economic constraints operating to greater or lesser degrees worldwide? Do these constraints suggest that we need to prioritise our research on the basis of maximising social or political impact rather than scientific merit?

SOME GUIDING PRINCIPLES FOR DEVELOPING A RESEARCH PROGRAMME

- Get the management agencies and public on board—The public generally views nature as the more visible components of biodiversity, such as trees, birds and mammals. However, conserving these species does not necessarily ensure the conservation of saproxylic insects. Dead wood may well support a fifth of all forest-dependent animals (Elton 1966, Grove 2002a), so its management is not a trivial conservation issue. Peer-reviewed science may not be enough to engage either the public or the agencies who manage land on the public's behalf. More populist articles, posters, leaflets, web sites, public presentations, field days for adults and children, and media appearances are likely to have greater impact, as long as the delivered message reflects our understandings as researchers so that scientific integrity is maintained. Social research may need to be considered as part of the overall research agenda alongside ecological research (Bartuska 2002).
- Use an adaptive management research framework where feasible—Much good ecological science is never implemented because it doesn't clearly suit the potential user, or is sidelined by politics and economics. Even conservation managers may prefer traditional methods over new scientific evidence (Pullin and others 2004). One of the most productive ways of progressing our understanding of saproxylic insects, while at the same time improving our chances of conserving them, is by encouraging incremental change through adaptive management (Jonsson and Kruys 2001). Using this process, one can begin to answer key management questions such as: (1) what should our goals be and how do we measure progress in reaching them?; (2) how can we most effectively take action to achieve conservation?; and (3) how can we learn to do conservation better? (Salafsky and others 2002). Active adaptive management has been defined as the systematic acquisition and application of reliable information to improve natural resource management over time (Wilhere 2002). Effectively, forestry or conservation management can be treated as a giant long-term ecological experiment. This means working with management agencies, to ensure that their management practices are documented along with the impacts they have on saproxylic insects or their habitat. Larsson and others (2005) present a case study of one such experiment. If the agencies can be persuaded to try a range of alternative management scenarios, their effectiveness can also be tested. One can also be opportunistic about the form studies take, by riding on the back of existing management plans or activities. One example would be to take advantage of tree-felling to learn about the habitat associations of saproxylic insects by sampling them directly from their habitat (Tavakilian and others 1997). By feeding back research findings to management agencies, management practices can evolve through a process akin to natural selection: the less desirable practices may be dropped while the better are propagated, because they are perceived as being both superior and more readily applicable to managers and policy makers (Grove and Stork 1999).
- Promote long-term monitoring—If management agencies are uncomfortable with researchers 'taking over' the forest, then establishment of dedicated research areas could be explored. The international network of Long Term Ecological Research (LTER) sites provides a useful model for targeting research to fill gaps in our ecological understanding (Grove 2004). Long-term monitoring is especially relevant to studies in forests because of the long time-frames in which ecological and management processes operate. Promoting long-term monitoring requires: (1) identifying innovative ways to secure long-term funding that can be guaranteed beyond typical political and institutional time-frames; and (2) education of funding bodies to ensure they recognise that useful results may take a prolonged period to obtain and that monitoring is not a second-rate science (Lindenmayer 1999).
- Promote interdisciplinary research—Saproxylic insects interact with other ecosystem components (especially fungi and dead wood), all of which are influenced by management. As Speight (1989) noted, "the relationships existing between saproxylic fungi and saproxylic invertebrates are clearly so intimate that the survival of members of one group is frequently dependent on the presence of members of the other…[however]…few accounts deal with fungi and invertebrates". Untangling these and other relationships requires researching more than just the insects, and may require researchers from a range of disciplines and with a range of skills. A cohesive package of research stands a greater chance of influencing management than does a disparate set of individual studies. This is the basis for Forestry Tasmania's coarse woody debris research package.
- Promote natural history and autecological studies—Many researchers shy away from natural history studies, yet an understanding of insect natural history is fundamental to understanding the many relationships between insects and their environment (Miller 1993), and hence the implications of our management of that environment. Autecological research has the potential to throw light on numerous aspects of a species' life relevant to conservation (Cheesman 2000). Where saproxylic insects are already scarce, it may be unethical or simply unfeasible to carry out statistically rigorous, fully replicated experiments, and strict codes of conduct may have to be applied to ensure that the species are not unduly threatened (Kirby and Drake 1993). Natural history studies can also help elucidate relationships between saproxylic insects and fungi. Even being able to define a species as saproxylic often requires knowledge of its natural history—and a lack of this knowledge can limit the analytical power of scientific studies (Grove 2002a, Yee and others 2005). Stable isotopes are increasingly being employed to ascertain the trophic level at which an organism feeds (Blüthgen and others 2003), and this is a field that could usefully be applied to putative saproxylic species.

- Promote advances in insect taxonomy—The 'taxonomic impediment' remains a constraint to our understanding of species and their ecological relationships (New 1996). There continues to be a lively debate about whether we really need to know the scientific names of all the insects that we work with, or whether parataxonomic units will suffice (Derraik and others 2002). Much depends on the use to which the resultant data are put (Krell 2004). For purely local studies (e.g., Basset and others 2004), a full scientific name may be superfluous, but for comparisons across studies or regions, they become more and more important. This presupposes that the species in question have been formally described—which in many parts of the world they have not. There is a global need for a sufficiently large pool of dedicated taxonomists to describe these species (Valdecasas and Camacho 2003). Identifying many saproxylic insect species currently requires great skill, plus access to comparative material which is not always readily available. Making taxonomic information more widely available through images and/or keys on the World Wide Web is a rapidly developing field. I have not referred to any particular web sites (because they change so frequently) but many of the relevant national and international research agencies are going down this route.
- Consider recent advances in insect surveillance—Methods for marking insects were reviewed recently (Hagler and Jackson 2001), and highlighted a number of advances that may be of interest to those studying saproxylic insects (see that paper for details). Additional techniques that deserve scrutiny include lasers to mark individual beetles (Griffiths and others 2001), and pheromone detectors to monitor otherwise inaccessible populations of rare insects (Svensson and others 2003). The time may fast be approaching when rapid chemical or genetic screening of samples for species-level information may come to our aid. With regard to these technologies, Gaston and O'Neill (2004) posit that "vision and enterprise are perhaps more limiting at present than practical constraints on what might possibly be achieved". For tracing individual insects, DNA-surveillance is also a possibility for the future, as now applied to whales (Baker and others 2003). The use of genetic markers is now an important tool in assessing insect dispersal ability (Sunnucks 2000, Watson 2003).
- Consider recent advances in software and hardware—Most present-day ecological studies are designed to be analysed with classical statistics. Yet advances in computing power increasingly allow the use of alternative approaches. These may appeal to those studying saproxylic insects, bearing in mind the frequent difficulties of fulfilling the requirements for classical analyses when studying species-rich assemblages or those where the most important species are rare or cryptic. Sometimes these new approaches are extensions to existing ones, enabling, for instance, the development of non-parametric probability estimates through randomisation procedures (e.g., Colwell and Coddington 1996, Manly 1997). Anderson (2001) and Anderson and Willis (2003) have extended their use by developing non-parametric multivariate equivalents of standard parametric univariate tests. But increasingly, techniques are available that make use of Bayesian statistics (Swinburne 2002, ter Braak and Etienne 2003), or use other non-classical statistics to explore, for example, effects of large-scale or unreplicated disturbances (Parr and Chown 2003). Another example is the development of software for determining the spatial scale of species' response to habitat fragmentation, again relying on randomisation procedures (Holland and others 2004). Modelling software is becoming more sophisticated, increasing its ease of use by mainstream ecologists (e.g., Muetzelfeldt and Massheder 2003) and/or increasing its power for complex analyses such as population viability analysis (Garrick and others 2004, Grimm and others 2004, Schtickzelle and Baguette 2004) and landscape-level prediction of habitat formation contingent on wildfire return intervals (Mackey and others 2002).

  Miniaturised electronics are finding increasing uses in field studies, too. For instance, probes attached to dataloggers could be used to record temperature or humidity at different depths within a log or tree hollow over extended periods. Self-contained 'iButtons' (Maxim/Dallas Semiconductor Corporation) can perform a similar function, and because they contain a transceiver the information can be uploaded to a computer or reader remotely. Cameras tripped by infra-red light beams could be used for photographing insects visiting hollows or flowers, rather than for the mammals which are the normal subject (e.g., Silveira and others 2003). Radio transmitters can now be made small enough to attach to individual beetles (Hedin and Ranius 2002), and GPS transmitters are also being manufactured smaller.

THE RESEARCH AGENDA

If, having considered the above, it is decided that further research on saproxylic insects, or the forests they inhabit, is warranted, then some suggestions follow. I have divided the ideas into 'ecological' and 'management' categories, depending on their focus, and have then grouped these ideas into three spatial scales at which the research is perhaps most appropriately conducted.

Ecologically Oriented Research: Small Scale

1. Developing standard techniques for sampling saproxylic insects—What are the relative merits of destructive versus passive sampling? What techniques are best for each of these types of sampling? Many papers have compared or promoted different techniques (e.g., Glen 1976, Grove 2000, Grove and Bashford 2003, Hanula and New 1996, Morewood and others 2002, Økland 1996, Owen 1992, Yee and others 2001). Factors to consider include the risks associated with disturbing or oversampling scarce species or their habitat; speed; selectivity; maintenance and sorting effort required; and the range of 'extra' ecological information obtained (Cheesman 2000). Different principles may operate in different regions, but the development of some standardised protocols would aid comparability among studies.
2. Autecological research on key saproxylic species—We will never understand the ecologies of every single saproxylic insect species, but in most regions it would be useful to know more about key species. 'Key' species might be defined as those with highest conservation needs, or those with a clearly important ecological role (e.g., ecosystem engineers, Jones and others 1996). Recent Fennoscandian examples where an understanding of

autecology has provided management insights include Jonsson (2003), Midtgaard and others (1998) and Ranius (2002). See the sections on insect surveillance and natural history above for further ideas.

3. Understanding relationships between saproxylic insects and fungi—These relationships are complex (Wilding and others 1989) and poorly understood in most regions, though Fennoscandia is relatively well served by recent studies (e.g., Jonsell and others 2001). How species-specific are fungus-insect relationships? Do saproxylic fungi depend on saproxylic insects any more or less than the insects depend on the fungi, or on the specific rotting wood types that they help to create (Yee and others 2005)? To what extent can we generalise about insect-fungus relationships from one species to the next, on the basis of taxonomic relatedness?

4. Understanding relationships between saproxylic insects and decomposition—Do ecosystems really need all these saproxylic insects? How much redundancy is there in the system (Srivastava 2002), and how would the forest function without them? Would fungi and other organisms be as efficient at breaking down decaying wood (and hence nutrient cycling) in the absence of saproxylic insects? Exclusion nets were used in a recent Finnish study (Müller and others 2002), and would seem to offer great potential for further studies.

5. Investigating the value of nectar sources for saproxylic insects—Many saproxylic insects emerge as adults and can be found at nearby flowers (Kirby 1992). To what extent are these nectar sources vital for their breeding success; are some plant species more important than others; and how near do they need to be to the larval habitat? This is more than a trivial issue in some heavily managed European forests, where nectar sources can be artificially low or where the survival of every individual member of a rare saproxylic insect species matters.

6. Investigating the value of burnt wood for saproxylic insects—Burnt wood is a natural component of many forest ecosystems, and an unnatural one in others. To what extent does it have unique values for saproxylic insects? And to what extent does burning intensity affect the ability of a log or standing dead tree to support saproxylic insects? These questions, and related ones on fungi, are the subject of recent studies in Fennoscandia (Penttilä and Kotiranta 1996; Wikars 2001, 2002) but other regions have apparently received less attention (though see Saint-Germain and others 2004 for a Canadian example). They would certainly be pertinent in Australia.

7. Investigating the value of dead wood for non-saproxylic insects—Dead wood is known to be important as a structural element for many terrestrial and aquatic plants and animals, but in terms of species numbers, is dead wood more or less important for non-saproxylic insects than for saproxylic insects? There have been some recent studies on the value of logs on the forest floor for non-saproxylic invertebrates (e.g., Andrew and others 2000, Evans and others 2003, Hanula and others 2005) but comparative studies are warranted.

Ecologically Oriented Research: Medium Scale

8. Investigating the extent of overlap in saproxylic insect faunas of logs, trees and litter—Which elements of a forest ecosystem deserve greatest conservation or management attention for saproxylic insects: logs on the ground, or the living or dead trees that generate the logs? There is some suggestion that this may vary by forest type (Grove 2002b). In many situations, we do not know the extent to which logs, old living trees and standing dead trees support different saproxylic insect assemblages, nor the extent to which apparently saproxylic species can utilise fine woody debris and litter (though see Nordén and others 2004 for fungi). In most parts of the world, we know little about the saproxylic insect fauna of tree hollows (though see Ranius 2002), compared to what we know about their use (probably at different spatial scales) by birds and mammals (Gibbons and Lindenmayer 2001). Schulz and Ammer (1996) have reported on the importance of upturned root plates for insect biodiversity, while Schiegg (2001) has compared the importance for saproxylic insects of logs derived from tree limbs and tree trunks. The fauna utilising subterranean dead wood (dead roots) is generally poorly known.

9. Investigating the role of fire in shaping saproxylic insect faunas—Fire can be a positive or a negative force for saproxylic insects (Enfrestøl 2003, Hanula and Wade 2003, Madoffe and others 2000, Moretti and Barbalat 2004, Wikars 1997), depending on the natural disturbance dynamics of the forest. In most regions we do not know what would be the implications for saproxylic insects of changing those dynamics. We often do not even know which species are fire-dependent rather than simply disturbance-dependent, but experiments such as those of Wikars (2002) can help us to find out.

Ecologically Oriented Research: Large Scale

10. Investigating the extent to which ecological traits among related saproxylic insect species are conserved across the globe—Given that we will never be able to investigate the autecology or natural history of more than a tiny proportion of the world's saproxylic species, to what extent can we deduce a species' ecology from that of related species studied elsewhere? There is some evidence for conservation of ecological traits among beetles (Leschen 2005), but a few studies across regions, for a range of saproxylic taxa, might further elucidate this.

Management Oriented Research: Small Scale

11. Investigating the value of artificially killed dead wood for saproxylic insects—Do artificially killed trees, branches or stumps offer the same opportunities for saproxylic insects as naturally killed ones? In some situations they probably do, because natural tree death can be as sudden as artificial tree death, for instance following a severe windstorm (Alexander 1994, Bouget and Duelli 2004) or hurricane (Whigham and others 1991). Likewise, in forests where wildfires are a major influence, silvicultural regeneration burns might be expected to offer some of the same opportunities to saproxylic insects as wildfires—though this requires investigation. But in other situations, trees only naturally fall over once major decay has set in, and the resultant dead wood is

likely to have different properties (structural, chemical and biological) from dead wood originating from felling a healthy tree (Boddy 2001). In these cases and some others, the result may be differences in saproxylic fauna (Shea and others 2002, Yee and others 2005). In other situations, trees may be deliberately wounded to provide habitat for saproxylic insects and other wildlife (Bull and others 1981, Green 1995), or stumps may be cut artificially high to leave additional habitat (Jonsell and others 2004). Are artificial stumps and wounds functional analogues for the real things? To what extent should we expect an intact saproxylic insect fauna to survive in a forest where artificial tree falls are the norm?

12. Investigating the value of relocating relocating saproxylic insects or the dead wood on which they depend. Should we seek to help endangered saproxylic insects recolonise lost ground, as those interested in lichens may do for their organisms (Lidén and others 2004)? More realistically, managers may need to relocate dead wood, either for conservation reasons (Grove and Tucker 2000) or for safety or aesthetic reasons. What factors determine its value for saproxylic insects in its new environment? For instance, to what extent does its positioning in a sunny or shady location affect its suitability for different species (Buisson 1999, Økland 2002), or for its rate of decay (Yin 1999)? Thermophilic organisms such as ants could clearly be affected by this (Higgins and Lindgren 2005). A range of similar questions applies to dead wood introduced into aquatic systems (Lester 2003, Lisle 2002, Wallace and Benke 1984), and to the choice of location for leaving standing dead trees in clearcuts (Sverdrup-Thygeson and Ims 2002).

Management Oriented Research: Medium Scale

13. Investigating dispersal and colonisation abilities of saproxylic insects—How readily can saproxylic insects colonise new habitat, and how is their ability to colonise influenced by factors such as flightedness, wing musculature, behaviour, physical distance, fragmentation and matrix quality (Bunnell and others 2002, Paradise 1998)? Are poor dispersers at more risk from human-induced fragmentation than good dispersers, or should those with intermediate powers of dispersal be of greatest concern? Is fragmentation leading to genetic losses or changes in surviving populations (Thomas and others 1998)? We can partially answer some of these questions for a few species (e.g., Ranius and Hedin 2001, Starzomski and Bondrup-Nielsen 2002, Watson 2003), but studies in other regions would also be beneficial so that we can better target the scale at which we manage for dead wood. Genetic markers (Garrick and others 2005, Sunnucks 2000) probably offer the best hope except for a few large (and perhaps rare) species, where direct surveillance of individuals is feasible (Ranius and Hedin 2001). New software may also prove valuable in inferring dispersal abilities by reinterpreting existing spatially explicit datasets for suites of saproxylic species (Holland and others 2004).

14. Developing appropriate criteria for the identification of important sites for saproxylic insects—In regions where the saproxylic insect fauna is well known, and where its conservation management is a major priority (e.g., the UK, Fennoscandia), there is a clearly defined need to prioritise sites for conservation. This requires collation of existing baseline information, and carrying out inventories for each key site (Cheesman 2000). The question then arises as to what to do with the information, which has limited value in its raw form. Alexander (2004) recommended the adoption of an index of ecological continuity, in which different saproxylic beetle species contribute different scores to the overall site index. The index correlates well with what have long been considered the 'best' (and usually the best protected) sites in England. Sverdrup-Thygeson (2001) found that the use of a similar index, based on fungi, to demarcate woodland key habitats in Norway did not fully capture the best sites for saproxylic beetles, suggesting that indices may need to be based on more than one taxonomic group. Despite this, the approach deserves greater consideration in other regions as knowledge of saproxylic insects (and fungi) increases.

15. Investigating the feasibility of using structural surrogates for saproxylic insect faunas—To what extent is it fair to use the occurrence of logs or old trees to gauge the suitability of a forest for saproxylic insects, or to monitor the effects of management (Stokland 2001)? It would generally be easier to monitor structural surrogates than to monitor the insects themselves (York 1999). In relatively intact forests, this may be appropriate (Grove 2002c) but does the relationship still hold in heavily modified ones?

16. Assessing the impact of fuelwood and firewood harvesting on saproxylic insects—The long-term collection of firewood can have major impacts on habitat availability for saproxylic insects (Hall and Farrell 2001), but there have been few scientific studies of its effects (Meggs 2002). The same presumably applies to industrial fuelwood, especially where it is harvested from native forests (Grove and Meggs 2003). It is sometimes difficult to persuade the public, or foresters, that such 'waste' wood deserves to be left in situ rather than harvested (Trockenbrodt and others 2002, Yee and others 2001). Further studies could only help.

17. Assessing the impact of feral saproxylic insects and other non-native species on native saproxylic insects—Other than pest species, feral saproxylic insects receive little attention, despite their widespread occurrence. Non-native bark beetles and longhorned beetles affect many parts of the world and are often the subject of control programmes, but what effect do they or other feral saproxylic species have on native species? Are they 'ecosystem engineers' (Crooks 2002)? For example, the feral weevil *Sipalus gigas* is one of the larger xylophagous insects in the rainforests of NE Queensland. Are there 'sleeper' feral saproxylic species that have yet to spread far, but which could potentially do so if steps are not taken to prevent them? A related issue concerns the effects of feral vertebrates on the dead wood resources that saproxylic insects require. In the UK, feral grey squirrels kill or wound many trees; is this harming or helping saproxylic species? In Australia, feral pigs root around amongst rotting logs, fragmenting them and consuming saproxylic insects directly. Feral lyrebirds in Tasmania similarly fragment rotting logs and redistribute fine woody debris on the forest floor in their search for invertebrates (Tanner 2000).

Management Oriented Research: Large Scale

18. Developing suitable landscape-scale predictive models—Forest managers traditionally model tree growth and yield, but tend not to consider tree death (other than by felling) and decay (Peng 2000). Ecologists are increasingly developing models for standing dead trees (Wilhere 2003) and coarse woody debris (Grove and others 2002, Mellen and Ager 2002, Rademacher and Winter 2003, Ranius and Kindvall 2004, Ranius and others 2003). Bringing the two model types closer together would increase the visibility of dead wood as a legitimate component of forest management (Mellen and others, 2002), and would increase model power. We could then begin to ask 'what if?' type questions with a direct relevance for saproxylic insects. For instance, what if climate change were to cause increases in log decay rates or tree growth rates or storm frequency (Opdam and Wascher 2004)? What if a pest outbreak were to cause mass tree mortality? What if forest policy were changed so that clearfell coupe size were reduced but coupe dispersion increased? What if fuelwood harvesting claimed an additional proportion of coarse woody debris that would otherwise be left after harvest?

    Another kind of modelling, population viability analysis, also promises to be a useful approach for saproxylic insects, as outlined above, especially if it can be linked to these other landscape-level modelling processes. Current software was mostly developed with vertebrates or plants in mind. It appears ill suited to modelling saproxylic insects (Jonsson and Kruys 2001) because if each log is treated as a patch, this creates too many patches for the analysis unless the spatial extent of the analysis is limited. Fox and others (2004) circumvented this problem in their study of a Tasmanian velvet-worm by treating each forestry coupe as a patch. Further research is needed to find ways around such limitations.

19. Developing techniques for maintaining or recreating forest landscapes suitable for saproxylic insects—The concept of 'new forestry', with its philosophy of maintaining complex ecosystems rather than simply the regeneration of trees (Franklin 1989), is increasingly being applied in many parts of the world (Armstrong and others 2003, Heitzman 2003, Larsson and others 2005, Lindenmayer and Franklin 2002). To what extent is it being successful in maintaining suitable conditions for saproxylic insects? In regions where habitat restoration is being pursued, what can be done to aid the restoration of suitable habitat for saproxylic insects across the forest landscape, beyond killing or wounding trees or relocating logs (see above)? Should the focus be on expanding existing sites of conservation importance? Should we consider translocation of saproxylic species to new sites beyond their dispersal range? Can we use studies of saproxylic insects of past forest landscapes as a guide to the future (Clark 2003; Whitehouse 2004, 2005)?

A CASE STUDY: FORESTRY TASMANIA'S COARSE WOODY DEBRIS RESEARCH PACKAGE

In Australia generally, managing production forests with the maintenance of CWD in mind requires a level of understanding of CWD that in most cases does not exist. In recognition of this, Forestry Tasmania (FT), as manager of Tasmania's state forests, has developed a research package comprising a number of related projects. These are aimed at (a) improving our understanding of the CWD resource and its dynamics; and (b) improving our understanding of the successional processes and habitat needs of CWD-dependent biodiversity. From these, the aim is (c) to develop management prescriptions at a range of scales, alongside suitable indicators to monitor their effectiveness. While some of the projects are being pursued in-house, most are collaborative or are being conducted by other agencies, with FT support. Details of the research package will be presented elsewhere, but the individual components are listed below:

A. Understanding the dead wood resource and its dynamics
    1. Harmonise methodologies for recording CWD in operational inventories
    2. Refine CWD model
    3. Improve model parameter estimates (decay rate, stag fall, fire-loss, CWD volume)
    4. Evaluate model robustness through sensitivity analysis and field validation

B. Understanding successional processes and habitat needs of dead wood dependent biodiversity
    1. Adopt curation standards for Tasmanian Forest Insect Collection
    2. Investigate role of fungal communities in CWD production in ageing trees
    3. Investigate effects of tree ageing on the development of structural complexity
    4. Determine the contribution of living trees of different ages as habitat for CWD-dependent invertebrates
    5. Evaluate relationship between log diameter and CWD-dependent biodiversity
    6. Determine overlap in CWD-dependent biodiversity between logs and trees of differing ages
    7. Investigate dispersal ability in a range of CWD-dependent species using genetic markers
    8. Investigate autecology of a range of CWD-dependent species of differing dispersal abilities
    9. Compare elements of CWD biodiversity in silvicultural and wildfire regrowth
    10. Evaluate the extent of fire dependence amongst CWD-dependent biodiversity

C. Developing prescriptions and suitable indicators to monitor their effectiveness
    1. Develop interim prescriptions and mitigation measures
    2. Develop a range of feasible landscape-level management scenarios
    3. Conduct population viability analyses for key CWD-dependent species
    4. Establish benchmark plots within the Warra LTER site to monitor CWD-dynamics over time

5. Develop a set of structural and biodiversity indicators (from outputs of A and B)
6. Simulate CWD dynamics and populations of key CWD-dependent species at the landscape level under different management scenarios to find optimal solutions
7. Refine interim prescriptions and mitigation measures based on landscape models
8. Validate indicators through field studies, refine and incorporate into FT management and planning systems

There is an infinite number of possible research questions that we could have sought to address in this package. We cannot afford to research something just because it is interesting, although having an interest in the research clearly helps levels of motivation. Our rationale has been to prioritise on the basis of (a) feasibility and (b) likely cumulative impact. For this reason, we have restricted our studies to one tree species, *Eucalyptus obliqua*, since this is ecologically and commercially the dominant species in the lowland wet eucalypt forests where forestry activities are particularly controversial. We have focused our research, where possible, at the Warra LTER site in southern Tasmania, because this enables individual projects to feed off one another and secures a level of funding that would not have been forthcoming had the projects been scattered around the State. *E.obliqua* forests are subject to periodic wildfires, and the main silvicultural intervention is clearfelling, followed by a hot burn and aerial reseeding with locally native eucalypt seed. They naturally have some of the highest volumes of CWD in the world, and levels can exceed 1000 m^3/ha after clearfelling, so CWD management is already a reality. We are bringing a different perspective to its management, from one that views CWD (or 'slash') as something to be reduced to acceptable levels through burning, or profitably harvested for fuelwood, to one that promotes CWD as habitat in need of sustaining across the forest landscape. Many members of the public see the current model of slash management as a sign of wasteful harvesting, but our stance is that it is ecologically more wasteful to remove it than is to leave it in the forest. But we are not out to shut forestry down. We are looking for solutions for the industry, rather than creating problems. We aim to 'have our cake and eat it'—to continue to manage these forests for timber and other products while sustaining adequate levels of CWD alongside other natural values

The reality is that research has different values for different sectors of society. For some senior agency officials and for government, we emphasise that the cost of this research is a small part of the price we pay for the social licence to continue doing business. Our research helps us to demonstrate that we manage the public forests sustainably and adaptively, through continuous improvement. Research projects are titled with this in mind. Many people are sceptical about forestry's intentions and integrity in Tasmania and would not normally credit Forestry Tasmania with this level of innovation. So we continue to promote our research widely, using language that can be understood by non-scientists. Accordingly we have presented the research package at public meetings and in the media, as well as through more academic channels such as our web site and university seminars.

There is also a sense that, when it comes to dead wood, simply doing the science is as important as finding new things out. By researching, and doing so openly, we are saying to the world, 'this stuff's important; we're prepared to spend our time, taxpayers' money and intellectual effort on it. We're lucky to have it. Value it!'

SUMMARY

No one research agenda will suit every region. Much depends on how the local forests work; how spatially diverse and expansive they are; what form human management of the forests has taken and for how long; how much is already know about the forests and their saproxylic insects; and what opportunities exist for research to inform management.

There is so much that we could research that I offered in this paper some guiding principles for selecting suitable projects. Getting the public, or at least the management agencies, on board is almost a prerequisite. Adaptive management is seen as a promising way forward for conducting research in 'real-life' situations. Research is likely to yield greater impact if it is interdisciplinary. Long-term monitoring is valuable because of the time-frames over which forests and forestry work. Insect taxonomy and natural history studies are often undervalued but provide a strong foundation for other research. Technological advances, for example in insect surveillance, computer software and electronic hardware, continue to extend the boundaries of what research is feasible.

Research can be broadly divided between 'ecologically' and 'management' oriented research, and considered at three spatial scales. Ecologically-oriented research may include: developing standard techniques for sampling saproxylic insects; autecological research on key saproxylic species; investigating relationships between saproxylic insects and fungi and between saproxylic insects and decomposition; elucidating the value of nectar sources and burnt wood for saproxylic insects; elucidating the value of dead wood for non-saproxylic insects; investigating the extent of overlap in saproxylic insect faunas of logs, trees and litter; investigating the role of fire in shaping saproxylic insect faunas; and investigating the extent to which ecological traits among related saproxylic insect species are conserved across the globe. More management-oriented research may include: investigating the value of artificially killed dead wood for saproxylic insects; investigating the value of relocating dead wood for saproxylic insects; investigating dispersal and colonisation abilities of saproxylic insects; developing appropriate criteria for the identification of important sites for saproxylic insects; investigating the feasibility of using structural surrogates for saproxylic insect faunas; assessing the impact of fuelwood and firewood harvesting on saproxylic insects; assessing the impact of feral saproxylic insects and other non-native species on native saproxylic insects; developing suitable landscape-scale predictive models; and developing techniques for maintaining or recreating forest landscapes suitable for saproxylic insects.

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LITERATURE CITED

Alexander, K.N.A. 1994. The use of freshly downed timber by insects following the 1987 storm. In: Kirby, K.J. and Buckley, G.P. (Ed.), Ecological responses to the 1987 great storm in the woods of South-East England. Peterborough, UK: English Nature, Science Report 23: 134-150.

Alexander, K.N.A. 2004. Revision of the index of ecological continuity as used for saproxylic beetles, Peterborough, UK: English Nature. Report 574.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology. 26: 32-46.

Anderson, M.J.; Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology. 84: 511-525.

Andrew, N.; Rodgerson, L.; York, A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral Ecology. 25: 99-107.

Armstrong, G.W.; Adamowicz, W.L.; Beck, J.A., Jr. [and others]. 2003. Coarse filter ecosystem management in a nonequilibrating forest. Forest Science. 49: 209-223.

Baker, C.S.; Dalebout, M.L.; Lavery, S.; Ross, H.A. 2003. WWW. DNA-surveillance: applied molecular taxonomy for species conservation and discovery. Trends in Ecology and Evolution. 18: 271-272.

Bartuska, A.M. 2002. Dead wood management issues and opportunities: future directions. In: Laudenslayer, W.F.Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 947-949.

Basset, Y.; Novotný, V.; Miller, S.E. [and others]. 2004. Conservation and biological monitoring of tropical forests: the role of parataxonomists. Journal of Applied Ecology. 41: 163-174.

Blüthgen, N.; Gebauer, G.; Fiedler, K. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia. 137: 426-435.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins. 49: 43-56.

Bouget, C.; Duelli, P. 2004. The effects of windthrow on forest insect communities: a literature review. Biological Conservation. 118: 281-299.

Buisson, R. 1999. Should deadwood be left in sun or shade? British Wildlife. 10: 342.

Bull, E.L.; Partridge, A.D.; Williams, W.G. 1981. Creating snags with explosives. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station.

Bunnell, F.L.; Wind, E.; Boyland, M. 2002. How should we spatially distribute dying and dead wood? In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 739-752.

Cheesman, O.D. 2000. Conservation of saproxylic invertebrates in the UK: a coordinated approach to BAP activities, and the wider research agenda. Wallingford, UK: CABI Bioscience.

Clark, S.H.E. 2003. Insect faunas associated with the fossil remains of *Pinus sylvestris* L. in blanket peat from northeast Scotland. Scottish Geographical Journal. 119: 39-52.

Colwell, R.K.; Coddington, J.A. 1996. Estimating terrestrial biodiversity through extrapolation. In: Hawksworth, D.L. (Ed.), Biodiversity: Measurement and Evaluation. London, UK: Chapman and Hall: 101-118.

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos. 97: 153-166.

Derraik, J.G.B.; Closs, G.P.; Dickinson, K.J.M. [and others]. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. Conservation Biology. 16: 1015-1023.

Elton, C. 1966. Dying and dead wood. In: Elton, C. (Ed.), The pattern of animal communities. London, UK: Methuen: 279-305.

Enfrestøl , A. 2003. Distribution of woody debris and saproxylic insects in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan. Masters thesis, Oslo, Norway: Agricultural University of Norway.

Evans, A.M.; Clinton, P.W.; Allen, R.B.; Frampton, C.M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management. 184: 251-262.

Fox, J.C.; Mesibov, R.; McCarthy, M.A.; Burgman, M.A. 2004. Giant velvet worm (*Tasmanipatus barretti*) in Tasmania, Australia: effects of planned conversion of native forests to plantations. In: Akcakaya, H.R.; Burgman, M.A.; Kindvall, O.; Wood, C.C.; Sjogren-Gulve, P.; Hatfield, J.S.; McCarthy, M.A., eds. Species conservation and management: case studies. New York: Oxford University Press: 150-161.

Franklin, J. 1989. Toward a new forestry. American Forests. 95: 37-44.

Garrick, R.; Sands, C.; Blacket, M. [and others]. 2006. Comparative phylogeography of saproxylic invertebrates. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22d International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Garrick, R.C.; Sands, C.J.; Rowell, D.M. [and others]. 2004. Phylogeography recapitulates topography: very fine-scale local endemism of a saproxylic 'giant' springtail at Tallaganda in the Great Dividing Range of south-east Australia. Molecular Ecology 13: 3315-3330.

Gaston, K.J.; O'Neill, M.A. 2004. Automated species identification: why not? Philosophical Transactions of the Royal Society of London, Series B. 359: 655-667.

Gibbons, P.; Lindenmayer, D. 2001. Tree hollows and wildlife conservation in Australia. Canberra, Australia: CSIRO Publishing.

Glen, D.M. 1976. An emergence trap for bark-dwelling insects, its efficiency and effects on temperature. Ecological Entomology. 1: 91-94.

Green, E.E. 1995. Creating decaying trees. British Wildlife. 6: 310-311.

Griffiths, G.; Winder, L.; Bean, D. [and others]. 2001. Laser marking the carabid *Pterostichus melanarius* for mark-release-recapture. Ecological Entomology. 26: 662-663.

Grimm, V.; Lorek, H.; Finke, J. [and others]. 2004. META-X: generic software for metapopulation viability analysis. Biodiversity and Conservation. 13: 165-188.

Grove, S.J. 2000. Trunk window trapping: an effective technique for sampling tropical saproxylic insects. Memoirs of the Queensland Museum. 46: 149-160.

Grove, S.J. 2002a. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation. 104: 149-171.

Grove, S.J. 2002b. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics. 33: 1-23.

Grove, S.J. 2002c. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecological Indicators. 1: 171-188.

Grove, S.J. 2004. Ecological research coverage at the Warra LTER site, Tasmania: a gap analysis based on a conceptual ecological model. Tasforests. 15: 43-54.

Grove, S.J.; Bashford, R. 2003. Beetle assemblages from the Warra log decay project: insights from the first year of sampling. Tasforests. 14: 117-129.

Grove, S.J.; Meggs, J. 2003. Coarse woody debris biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. Australian Forestry. 66: 258-272.

Grove, S.J.; Meggs, J.; Goodwin, A. 2002. A review of biodiversity conservation issues relating to coarse woody debris management in the wet eucalypt production forests of Tasmania. Hobart, Australia: Forestry Tasmania.

Grove, S.J.; Stork, N.E. 1999. The conservation of saproxylic insects in tropical forests: a research agenda. Journal of Insect Conservation. 3: 67-74.

Grove, S.J.; Tucker, N. 2000. The importance of mature timber habitat in forest management and restoration: what can insects tell us? Ecological Management and Restoration. 1: 68-69.

Hagler, J.R.; Jackson, C.G. 2001. Methods for marking insects: current techniques and future prospects. Annual Review of Entomology. 46: 511-543.

Hall, T.E.; Farrell, T.A. 2001. Fuelwood depletion at wilderness campsites: extent and potential ecological significance. Environmental Conservation. 28: 241-247.

Hanula, J.L.; Horn, S.; Wade, D.D. 2006. The role of dead wood in maintaining arthropod diversity on the forest floor. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22d International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Hanula, J.L.; New, K.C.P. 1996. A trap for capturing arthropods crawling up tree boles, Research Note SRS-3. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station.

Hanula, J.L.; Wade, D.D. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. Forest Ecology and Management. 175: 163-184.

Hedin, J.; Ranius, T. 2002. Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. Computers and Electronics in Agriculture. 35: 171-180.

Heitzman, E. 2003. “New forestry” in Scotland. Journal of Forestry. 101: 36-39.

Higgins, R.J.; Lindgren, B.S. 2006. The fine-scale attributes of coarse woody debris associated with utilization by ants. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22d International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Holland, J.D.; Bert, D.G.; Fahrig, L. 2004. Determining the spatial scale of species’ response to habitat. Bioscience 54: 227-233.

Jones, C.G.; Lawton, J.H.; Shachak, M. 1996. Organisms as ecosystem engineers. pp.130-147 *In*: Samson, F. B.; Knopf, F. L., eds. *Readings in Ecosystem Management.* Springer-Verlag, New York. (Reprinted from Jones, C. G.; Lawton, J. H.; Shachak, M. 1994. Organisms as Ecosystem Engineers. Oikos 69: 373-386).

Jonsell, M.; Nitterus, K.; Stighall, K. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation. 118: 163-173.

Jonsell, M.; Nordlander, G.; Ehnström, B. 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. Ecological Bulletins. 49: 173-194.

Jonsson, B.G.; Kruys, N. 2001. Ecology of coarse woody debris in boreal forests: future research directions. Ecological Bulletins. 49: 279-281.

Jonsson, M. 2003. Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. Ecological Entomology. 28: 159-167.

Kirby, K.J.; Drake, C.M. 1993. Annex 1 in dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. Peterborough, UK: English Nature.

Kirby, P. 1992. Habitat management for invertebrates: a practical handbook. Sandy, UK: Royal Society for the Protection of Birds.

Krell, F.-T. 2004. Parataxonomy vs. taxonomy in biodiversity studies—pitfalls and applicability of ‘morphospecies’ sorting. Biodiversity and Conservation. 13: 795-812.

Larsson, S.; Ekbom, B.; Schroeder, L.M.; McGeoch, M.A. 2006. Saproxylic beetles in a boreal forest landscape managed for coarse woody debris. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22d International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Laudenslayer, W.F., Jr.; Shea, P.J.; Valentine, B. [and others], eds. 2002. The ecology and management of dead wood in western forests. Proceedings of a Symposium, Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station.

Leschen, R. 2006. Wood, elytra, and antiquity: geologic and phylogenetic history of dead wood coleoptera. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22d International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Lester, R. 2003. Wood to water: the effectiveness of re-introduction of woody debris as a biodiversity enhancement tool in streams in agricultural environments. Monash, Australia: Monash University.

Lidén, M.; Pettersson, M.; Bergsten, U.; Lundmark, T. 2004. Artificial dispersal of endangered epiphytic lichens: a tool for conservation in boreal forest landscapes. Biological Conservation. 118: 431-442.

Lindenmayer, D.B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. Forest Ecology and Management. 115: 277-287.

Lindenmayer, D.B.; Franklin, J.F. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Washington, DC: Island Press.

Lisle, T.E. 2002. How much dead wood in stream channels is enough? In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E. eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 85-94.

Mackey, B.; Lindenmayer, D.; Gill, M. [and others]. 2002. Wildlife, fire and future climate: a forest ecosystem analysis. Collingwood, Australia: CSIRO Publishing.

Madoffe, S.S.; Bakke, A.; Tarimo, J.A. 2000. The effect of fire on the diversity and abundance of wood-living beetles in a miombo woodland, Tanzania. Southern African Forestry Journal. 187: 51-57.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte-Carlo methods in biology, 2nd Edition. London, UK: Chapman and Hall.

Meggs, J.M. 2002. Potential impacts of firewood harvesting on invertebrate biodiversity. In: Miller, J. (Ed.), Firewood Conferences 2000-2002. Hobart, Australia: Tasmanian Conservation Trust: 178-181.

Mellen, K.; Ager, A. 2002. A coarse woody debris dynamics model for the western Cascades. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 503-516.

Mellen, K.; Marcot, B.G.; Ohmann, J.L. [and others]. 2002. DecAID: a decaying wood advisory model for Oregon. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E. [eds.], Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 527-534.

Mesibov, R. 1994. Faunal breaks in Tasmania and their significance for invertebrate conservation. Memoirs of the Queensland Museum. 36: 133-136.

Midtgaard, F.; Rukke, B.A.; Sverdrup-Thygeson, A. 1998. Habitat use of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae): effect of basidiocarp size, humidity and competitors. European Journal of Entomology. 95: 559-570.

Miller, J.C. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. Biodiversity and Conservation. 2: 233-241.

Moretti, M.; Barbalat, S. 2004. The effects of wildfires on wood-eating beetles in deciduous forests on the southern slope of the Swiss Alps. Forest Ecology and Management. 187: 85-103.

Morewood, W.D.; Hein, K.E.; Katinic, P.J.; Borden, J.H. 2002. An improved trap for large wood-boring insects, with special reference to *Monochamus scutellatus* (Coleoptera: Cerambycidae). Canadian Journal of Forest Research. 32: 519-525.

Muetzelfeldt, R.; Massheder, J. 2003. The Simile visual modelling environment. European Journal of Agronomy. 18: 345-358.

Müller, M.M.; Varama, M.; Heinonen, J.; Hallaksela, A.-M. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. Forest Ecology and Management. 166: 165-181.

New, T.R. 1996. Taxonomic focus and quality control in insect surveys for biodiversity conservation. Australian Journal of Entomology. 35: 97-106.

Nordén, B.; Ryberg, M.; Gotmark, F.; Olausson, B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation. 117: 1-10.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology. 93: 195-209.

Økland, B. 2002. Canopy cover favours sporocarp-visiting beetles in spruce forests. Norwegian Journal of Entomology. 49: 29-39.

Opdam, P.; Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation. 117: 285-297.

Owen, J.A. 1992. Experience with an emergence trap for insects breeding in dead wood. British Journal of Entomology and Natural History. 5: 17-20.

Paradise, C.J. 1998. Colonization and development of insects in simulated treehole habitats with distinct resource and pH regimes. Ecoscience. 5: 39-45.

Parr, C.L.; Chown, S.L. 2003. Burning issues for conservation: a critique of faunal fire research in southern Africa. Austral Ecology. 28: 384-395.

Peng, C. 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management. 132: 259-.

Penttilä, R.; Kotiranta, H. 1996. Short-term effects of prescribed burning on wood-rotting fungi. Silva Fennica. 30: 399-419.

Pullin, A.S.; Knight, T.M.; Stone, D.A; Charman, K. 2004. Do conservation managers use scientific evidence to support their decision-making? Biological Conservation. 119: 245-252.

Rademacher, C.; Winter, S. 2003. Coarse woody debris in natural beech forests: generic predictions of the simulation model BEFORE-CWD of quantity, spatial distribution and availability. Forstwissenschaftliches Centralblatt. 122: 337-357.

Ranius, T. 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodiversity and Conservation. 11: 931-941.

Ranius, T.; Hedin, J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia. 126: 363-370.

Ranius, T.; Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation. 119: 51-59.

Ranius, T.; Kindvall, O.; Kruys, N.; Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. Forest Ecology and Management. 182: 13-29.

Saint-Germain, M.; Drapeau, P. Hebert, C. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of Northeastern North America. Biological Conservation. 118: 583-592.

Salafsky, N.; Margoluis, R.; Redford, K.H.; Robinson, J.G. 2002. Improving the practice of conservation: a conceptual framework and research agenda for conservation science. Conservation Biology. 16: 1469-1479.

Schiegg, K. 2001. Saproxylic insect diversity of beech: limbs are richer than trunks. Forest Ecology and Management. 149: 295-304.

Schtickzelle, N.; Baguette, M. 2004. Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. Oikos. 104: 277-290.

Schulz, U.; Ammer, U. 1996. Opened root plates and their contribution to the insect biodiversity of forests. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie. 11: 677-681.

Shea, P.J.; Laudenslayer, W.F., Jr.; Ferrell, G.; Borys, R. 2002. Girdled versus bark beetle-created ponderosa pine snags: utilization by cavity-dependent species and differences in decay rate and insect diversity. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds., Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 145-154.

Silveira, L.; Jacomoa, A.T.A.; Diniz-Filho, J.A.F. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation. 114: 351-355.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Strasbourg, France: Council of Europe.

Srivastava, D.S. 2002. The role of conservation in expanding biodiversity research. Oikos. 98: 351-360.

Starzomski, B.M.; Bondrup-Nielsen, S. 2002. Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae). Ecoscience. 9: 20-27.

Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins. 49: 71-84.

Sunnucks, P. 2000. Efficient genetic markers for population biology. Trends in Ecology and Evolution. 15: 199-203.

Svensson, G.P.; Larsson, M.C.; Hedin, J. 2003. Air sampling of its pheromone to monitor the occurrence of *Osmoderma eremita*, a threatened beetle inhabiting hollow trees. Journal of Insect Conservation. 7: 189-198.

Sverdrup-Thygeson, A. 2001. Can 'continuity indicator species' predict species richness or red-listed species of saproxylic beetles? Biodiversity and Conservation. 10: 815-832.

Sverdrup-Thygeson, A.; Ims, R.A. 2002. The effect of forest clear-cutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation. 108: 347-357.

Swinburne, R. 2002. Bayes's theorem. Oxford, UK: Oxford University Press.

Tanner, Z. 2000. Ecological impacts of the superb lyrebird in Tasmania. Honours thesis. Hobart, Australia: University of Tasmania.

Tavakilian, G.; Berkov, A.; Meurer-Grimes, B.; Mori, S. 1997. Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guyana. The Botanical Review. 63: 303-355.

ter Braak, C.J.F.; Etienne, R.S. 2003. Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. Ecology. 84: 231-241.

Thomas, C.; Hill, J.; Lewis, O. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology. 67: 485-497.

Trockenbrodt, M.; Imiyabir, Z.; Josue, J. 2002. Hollow logs and logging residues from Deramakot Forest Reserve, Sabah, Malaysia. Forest Ecology and Management. 165: 141-150.

Valdecasas, A.G.; Camacho, A.I. 2003. Conservation to the rescue of taxonomy. Biodiversity and Conservation. 12: 1113-1117.

Wallace, J.; Benke, A. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. Canadian Journal of Fisheries and Aquatic Sciences. 41: 1643-1652.

Watson, S. 2003. Dispersal and gene flow in *Prostomis atkinsoni* (Coleoptera). Honours thesis. Melbourne, Australia: LaTrobe University.

Whigham, D.F.; Olmsted, I.; Cabera Cano, E.; Harmon, M.E. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatán Peninsula. Biotropica. 23: 434-441.

Whitehouse, N.J. 2004. Mire ontogeny, environmental and climatic change inferred from fossil beetle successions from Hatfield Moors, eastern England. Holocene. 14: 79-93.

Whitehouse, N.J. 2006. What can forest managers learn from research on subfossil insects? In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22[d] International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Wikars, L.-O. 1997. Pyrophilous insects in Orsa Finnmark, Central Sweden: biology, distribution, and conservation (Brandinsekter i Orsa Finnmark: biologi, utbredning och artbevarande). [In Swedish, with English summary]. Entomologisk Tidskrift. 118: 155-169.

Wikars, L.-O. 2001. The wood-decaying fungus *Daldinia loculata* (Xylariaceae) as an indicator of fire-dependent insects. Ecological Bulletins. 49: 263-268.

Wikars, L.-O. 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation. 6: 1-12.

Wilding, N.; Collins, N.M.; Hammond, P.M.; Webber, J.F. 1989. Insect-fungus interactions. London, UK: Academic Press.

Wilhere, G.F. 2002. Adaptive management in habitat conservation plans. Conservation Biology. 16: 20-29.

Wilhere, G.F. 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. Forest Ecology and Management. 174: 521-539.

Wu, J.G.; Hobbs, R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecology. 17: 355-365.

Yee, M.; Grove, S.J.; Richardson, A.; Mohammed, C. 2006. Brown rot in inner heartwood: why large logs support characteristic saproxylic beetle assemblages of conservation concern. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Yee, M.; Yuan, Z.-Q.; Mohammed, C. 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. Tasforests. 13: 119-128.

Yin, X.W. 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. Oecologia. 121: 81-98.

York, A. 1999. Ecologically sustainable management: the utility of habitat surrogates for assessing terrestrial invertebrate diversity in temperate forests. In: Ponder, W.; Lunney, D., eds. The other 99%: the conservation and biodiversity of invertebrates. Mossman, Australia: Royal Zoological Society of New South Wales: 34-39.