Conservation Through Management – Cut Wood as Substrate for Saproxylic Organisms

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Abstract

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The experience of naturalists indicate that many forest species have become more rare as a result of intensive forest management. As less dead wood is one of the key changes in most forests, saproxylic organisms tend to be especially vulnerable. So far, countermeasures have focused on setting aside reserves and key-habitats. However, while unmanaged reserves are likely to be important for many species, such areas provide little substrate for organisms adapted to habitats created by recent fires or other stand-level disturbances. Such species potentially benefit more from increased production and retention of dead wood in managed forest landscapes.

This thesis evaluates artificially created high stumps as hosts for saproxylic beetles, and stumps and logs as substrates for saproxylic fungi. The studies are based on seven years of data from cut wood of various tree species, diameters and conditions of sun-exposure in Fagerön (Uppland, Sweden). The results demonstrate that hundreds of beetle species, including many red-listed species, utilise high stumps, and that two thirds of this fauna favours stumps in semi- or fully sun-exposed conditions. Thus, high stumps in logging areas and other open sites are potentially very valuable tools for conservation of saproxylic beetles. Cut wood, especially large diameter logs, also hosted numerous species of saproxylic fungi. Generally, most such species were little influenced by exposure. Thus, cut logs may support fungal diversity, both in managed forest landscapes and in forest reserves and key-habitats.

Key words: Biodiversity conservation, Coarse woody debris, Forest dynamics, Fungal succession, Wood decay

It was a foggy, cloudy morning, and a dun-coloured veil hung over the house-tops, looking like the reflection of the mud-coloured streets beneath. My companion was in the best of spirits, and prattled away about Cremona fiddles, and the difference between a Stradivarius and an Amati. As for myself, I was silent, for the dull weather and the melancholy business upon which we were engaged, depressed my spirits.

'You don't seem to give much thought to the matter in hand' I said at last, interrupting Holmes' musical disquisition.

'No data yet' he answered. 'It is a capital mistake to theorise before you have all the evidence. It biases the judgement.'

Sir Arthur Conan Doyle: *A study in scarlet*.

Contents

Appendix

Papers I-IV

This thesis is based on the following papers, which will be referred to by their respective Roman numerals.

I.   Schroeder, L.M., Weslien, J., Lindelöw, Å. & Lindhe, A. 1999. Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. *Forest Ecology and Management 123:* 21-30.

II.   Lindhe, A., Åsenblad, N. & Toresson, H.-G. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. *Biological Conservation*, in press.

III.   Lindhe, A., Lindelöw, Å. & Åsenblad, N. Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter. Manuscript.

IV.   Lindhe, A. & Lindelöw, Å. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Manuscript.

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Introduction

Although institutionalised efforts to protect nature date back to the beginnings of the last century, conservation biology related to forests is a young discipline, its coming of age in Sweden represented by the first IUCN-adapted Red Lists and their associated educational materials (Ingelög et al. 1984; Ehnström and Waldén 1986). Together with Red Lists from other Scandinavian countries, these materials were internationally quite unique in their emphasis on insects, bryophytes, lichens and fungi, perspectives that reflect relatively species-poor and well-known faunas and floras. Focusing on the remaining old-growth habitats, logging was routinely classified as the main threat for most species. While some insects and plants were recognised as being adapted to burnt wood and soil, the fundamental implications of fire dynamics in natural forest landscapes (Zackrisson 1977; Granström 1993, 1996; Schimmel and Granström 1996, 1997; Linder and Östlund 1998) had yet to impact the Scandinavian conservation community.

Meanwhile, data on insect species that benefit from, or even depend on, habitats created by natural or artificial disturbances (e.g. Saalas 1917; Forsslund 1934; Palm 1955) grew as new information accumulated. Lundberg (1984) reviewed saproxylic beetles (beetles utilising dead wood and associated fungi) adapted to burnt habitats, and Wikars (1992) published the first of several works on insects adapted to dead wood and fungi of fire-sites. In Denmark, Martin (1989) drew attention to the detrimental effects of closing canopies and encroachment of former solitary trees to the click beetle fauna. A couple of years later in Sweden, Gärdenfors and Baranowski (1992) argued that saproxylic oak-species (as opposed to beech fauna) should be adapted to sun-exposed conditions (predictions partly confirmed by Ranius and Jansson 2000). In boreal and hemi-boreal settings, Wikars and Ås (1991) and Ahnlund and Lindhe (1992) demonstrated that not only fire-sites, but also logging areas with enough suitable substrate could host many red-listed saproxylic beetles.

Dynamics also gained attention among foresters, and models were developed using historical fire disturbance regimes as templates for landscape planning and management (Angelstam et al. 1993; Angelstam 1998). However, having witnessed decades of landscape-transforming, stereotype forestry, many environmentalists had a deep scepticism against disturbances in general and logging in particular. This position was nourished as initiatives like 'One step ahead' (Karström 1992) and educational programmes for forest authority staff spread the ability to identify a number of rare fungi, mosses and lichens outside a small circle of specialists. Many such species are associated with old-growth forests presumed to have experienced long-term stand level continuity (e.g. Olsson and Gransberg 1993), a pattern that was sometimes assumed to characterise rare forest organisms in general. Conceptually related, the national survey of 'key-habitats' for forest biodiversity, initiated in the early nineties, relied heavily upon indicator species chosen from bryophytes, lichens and fungi (Nitare and Norén 1992). Operational in closed-canopy spruce forest habitats, the methodology was less suited to detect values in temporary habitats and open forests generated by large-scale disturbances. While fire-sites were included in the survey, the concept of logging

sites as potential key-habitats for organisms adapted to natural forest dynamics had few proponents at this time.

By the early nineties a modest amount of 'mimicking of natural disturbances' by leaving some retention trees, as well as smaller patches of intact forest, on logging sites had become standard procedures of main-stream forestry. A certain amount of active creation of dead wood was also commonly practised, as some stumps, a couple of metres high, were cut from living trees to serve as habitat (mainly) for saproxylic beetles. Such high stumps however, had been introduced largely on intuitive grounds, and there were as yet no data on utilisation by saproxylic organisms. Thus, this study was set up specifically to evaluate the potential of high stumps (and, to some extent, cut logs) as tools for conservation of saproxylic beetles and fungi. By doing so, the experiment also came to touch upon more general issues of responses to forest disturbances and the conservation potential of 'artificially' created as opposed to natural, forest elements.

Materials and methods

Site

With active support from the forest owner Hargs' bruk and the regional environmental authorities, the study site was located to Fagerön, an area on the Baltic coast of the province Uppland, (600 12' N - 180 27' E) known to host a high diversity of organisms from various taxa. Five rectangular 50 x 100 m plots where delineated in stands of mixed, unmanaged, secondary forests. In February and March 1994, half of each plot was 'thinned' (more trees were cut than in normal commercial thinning operations) and the other half 'clear-cut' with a machine harvester. On and around the plots, living trees of spruce, birch, aspen and oak were cut to produce a total of 130 four metre stumps, as well as 70 pairs of one metre stumps and three metre logs. The substrates represented medium to large (0.23-0.65 m) diameters and various conditions of shade and sun-exposure.

Study organisms and sampling

Fungi: All stumps and logs were inspected for presence of macroscopic fruit bodies of saproxylic Ascomycetes and Basidiomycetes during one day in October each year from 1995 to 2003. (This survey is planned to continue). Specimens that were not readily identifiable in the field were later examined with a microscope so that all but a very small number of severely degraded fruit bodies could be identified to species. As fungi are present also as mycelia in the wood without producing fruit bodies (Johannesson and Stenlid 1999; Vainio and Hantula 2000), data represent minimum estimates of species presence in the wood.

Beetles: To document, as thoroughly as possible, the saproxylic fauna occurring in the area during the time of the study, barrier traps filled with diluted propylene glycol were attached to all 270 experimental stumps and logs during the flight season from the end of April to late August 1994-1998.

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Sampling of beetles that utilised the four metre stumps as breeding substrates was initiated in 1995. The stumps were divided into two similarly composed cohorts. In order to target only insect individuals directly associated with the substrate, the stumps of one cohort were enclosed in large, fine-meshed nylon net sacks during the flight season of most species. Enclosed and open cohorts alternated between years, so that each individual stump was open to egg-laying by free-flying females one season and enclosed the next. Insects emerging from the stumps were caught in traps within the enclosures. All stumps were left open in 1999, and sampling was resumed in 2000 and 2001. Thus by the end of the experiment, each stump had been enclosed for three seasons (1995, 1997, 2000, or 1996, 1998, 2001).

While the experimental design had the advantage of following specific stumps over a period of time, there were some drawbacks. Firstly, biannual enclosing substantially modified natural patterns of succession as access by egg-laying females from the outside was blocked every other year between 1995 and 1998. Secondly, species that normally develop for two years in the stumps were drastically under-sampled 1996-1999 as, during this period, all two-year individuals emerged during years of non-enclosure. However, since the intention was to compare species and substrates in relative rather than absolute terms, these implications were not regarded as a major problem for our purposes.

Complementary surveys of galleries and exit holes to assess the reproduction of bark beetles in the stumps and logs were performed by the end of the first and second season after cutting. To assess the efficiency of trapping in relation to the real production, all four metre stumps of spruce and aspen were surveyed for characteristic exit holes of some species after the last field season in 2002.

Sun-exposure

As light conditions were expected to vary a great deal, even within subplots of similar cutting intensities, we assessed the exposure conditions of each stump separately by measuring the seasonal evaporation from small water-filled glass vessels for 6-8 weeks during the summers of 1996, 1997 and 1998. The evaporated volumes were transformed to annual indices ranging from 0 to 1. Annual indices for individual stumps were well correlated between years, and final indices of relative exposure for each stump were calculated as means over three seasons. To maintain conditions of exposure until the end of the experiment, re-growth around the stumps in the clear-cut plots was removed in 1999.

As predicted, there was much exposure variation, especially within thinned stands and on clear-cuts, due to shading from nearby retention trees and forest edges on the small plots. However, mean indices for intact forest, thinned sub-plots and clear-cuts were well separated and significantly different. As 90% of the indices from stumps in intact forest were ≤ 0.33, this value was used as a threshold in the categorised models (see below) to separate semi- and fully exposed conditions generated by disturbances from the shaded conditions characteristic of closed-canopy stands.

Data analysis

Fungi: Numbers of saproxylic species recorded 1995-2002 in relation to object category (log / 1-m stump / 4-m stump), tree species, diameter and exposure were modelled using ANCOVA. Distributions of individual species of fungi related to diameter and exposure were analysed based on presence / absence data from relevant host tree species using binary response logistic regression models. To illustrate the succession of individual species, 'peak times of occurrence', expressed as number of seasons after cutting, were calculated for all species recorded $\geq$ 20 times during the study period. Numbers of species, records accounted for by the ten most frequent species, and the percentage of species represented by one record only (singletons), were calculated based on a two-step rarefaction process to compensate for differences in numbers of objects and records. Similar procedures were used to analyse numbers of species on different object categories, and the percentage of these species that were unique to each category.

Beetles: Numbers of saproxylic species and red-listed species recorded 1995-2001, per stump and per stump mantle area, were modelled in relation to tree species, stump diameter, exposure and diversity of saproxylic fungi using ANCOVA. These models were also used to extrapolate numbers of species and red-listed species, per stump and mantle area, in standardised 'large' and 'medium', as well as 'sun-exposed' and 'shaded' stumps. A similar model was used to analyse the proportion of red-listed species recorded from each stump. Species accumulation curves for each tree species, and relative Sörenson's similarity indices for different pairs of tree species, were calculated by rarefaction procedures.

Eighty-five beetle species including six red-listed species, a total of more than 35 000 individuals, were selected for species-specific analysis. To focus on the most relevant hosts for each beetle, tree species with densities less than half of that recorded from the main host were excluded. Densities from relevant host trees were analysed in relation to diameter and exposure using linear Poisson regression models. As there were indications of non-linear responses to exposure in a number of cases, categorised Poisson regression models were used as complements to compare densities in semi-/fully exposed conditions (> 0.33) with densities in closed-canopy shade ($\leq$ 0.33).

To compare the species in the analyses with the full set of species recorded in the study, as well as to compare red-listed and non red-listed species, the mean diameter and exposure per individual were calculated for each recorded species, weighting all species equally regardless of sample size. Grand means for each group were compared with ANOVA and Tukey Simultaneous Tests.

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Main results

Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting (I)

Main questions addressed by the study:
1. How similar are cut high stumps and naturally created snags in terms of species compositions and attack patterns of bark- and wood-boring beetles?
2. How are attack rates on cut high stumps influenced by time of cutting, stump diameter and stump height?
3. Are there differences in spruce bark beetle utilisation between stumps and logs?
4. Does the presence of cut high stumps increase the risk for attacks on living trees by bark- and wood-boring beetles?

High stumps and logs of spruce from Fagerön (hemi-boreal zone) and high stumps of spruce from Grangärde (southern boreal zone) were surveyed for galleries and exit holes of pioneer beetle species, especially bark beetles, by the end of the first and second seasons after cutting. In contrast to results of earlier studies of snow- or wind-broken stumps, most objects in our study were colonised by saproxylic beetles already during the first summer, and all were colonised after the second summer. We found that *Monochamus sutor* reproduced in a considerable proportion of the Grangärde (but not Fagerön) stumps, whereas no attacks by this species have been reported from earlier studies of standing dead spruce outside burnt areas. Also, *Ips typographus* colonised larger proportions of stumps in both areas than previously reported from naturally broken trees. These differences may reflect a concentration of attacks on the relatively low volumes of cut stumps compared to the volumes of broken trees following massive storm-fellings, as well as the benign sun-exposed conditions of clear-cuts compared to stands.

Utilisation was also influenced by the time of cutting. In Grangärde, where both spring- and autumn-cut stumps were present, *I. typographus* was only found in spring-cut stumps, while *Orthomicus spp.* and *Hylurgops palliatus* significantly favoured autumn-cut stumps. In Fagerön, where both logs and stumps (all spring-cut) were present, *I. typographus* attacked a significantly higher proportion of logs than stumps, and utilised significantly larger bark areas on logs than on stumps. *I. typographus* preferred large, rather than medium diameter logs, a result in accordance with those of earlier studies, while results related to stump height were inconclusive.

Although high stumps in both localities were utilised by *I. typographus* to a larger extent than has been demonstrated for natural stumps and snags created by wind or snow, levels of attack were still moderate. Obviously, 'artificial' high stumps are far from ideal breeding substrates for the species, and there is little risk that such stumps generate enough individuals to damage living trees. Later experimental studies of fallen spruce on clear-cuts (a much better substrate for *I. typographus* than stumps) by Hedgren et al. (2003) indicate that these conclusions

are valid also for considerably higher densities of stumps than are commonly created at logging sites today.

Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession (II).

Main questions addressed by the study:
1. What characterise fungal communities on cut substrates in terms of species composition, species frequency and succession?
2. Are there differences between logs and high stumps in terms of numbers and accumulation of species?
3. How is the diversity of fungi affected by tree species, wood diameter and sun-exposure?

A total of 148 species of saproxylic fungi, including 7 red-listed species (Gärdenfors 2000) were recorded from logs and stumps of spruce, birch, aspen and oak between 1995 and 2002. These species represent approximately 6% of the estimated number of Swedish Ascomycetes and Basidiomycetes considered as obligatory saproxylic (information from the Swedish Species Information Centre).

The ten most common species accounted for 50% of the records from object of all categories and tree species, while 39% of the species were recorded from one object only. Adjusting for differences in numbers of objects and records, percentages were fairly similar for all tree species. Comparable data from natural substrates are confined to fallen spruce. These indicate no major differences between naturally dead trees and the cut logs in our study in terms of numbers of species (Lindblad 1998), or proportions of frequently occurring species and species recorded only once (Høiland and Bendiksen 1996). Moreover, many species that were frequently recorded from logs in our study, like *Stereum sanguinolentum, Trichaptum abietinum, Phlebiopsis gigantea* and *Antrodia serialis* on spruce, and *Chondrostereum purpureum, Stereum hirsutum* and *Trametes spp.* on deciduous trees, are characteristic colonisers of natural windfalls (Niemelä et al. 1995). Thus, at least cut logs seem to host fungal communities not fundamentally different from those on comparable, naturally fallen trees.

Fruit bodies developed rapidly on most substrates but oak 4-m stumps that stood out as 'slow starters'. There was a distinct succession of species, primary colonisers gradually being replaced by more secondary species as decomposition proceeded. Individual species peaked first on logs, then on 1-m stumps and last on 4-m stumps. This pattern may result from logs dying faster than stumps, from more benign moisture conditions in the wood of logs compared to stumps, and/or from fungal colonisation of logs by mycelia present in the soil. Almost half of all species recorded from spruce were confined to this host, while most common species on deciduous substrates were generalists that were found on more than one tree species. The highest level of similarity was found between birch and aspen.

Logs hosted significantly richer fungal communities than 1-m stumps and 4-m stumps (mean numbers of species 8.0, 6.0 and 4.6, respectively), including all red-listed species encountered 1995-2002. Logs also had a slightly higher rate of species turnover. However, many high stumps hosted large fruit bodies of common

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species like *Fomitopsis pinicola, Trichaptum abietinum* and *Fomes fomentarius* that provide breeding habitats or nutrition for large numbers of saproxylic insects (Jonsell 1999 and references therein). These species may also act like precursors for rarer fungi that utilise wood in later stages of decay, e.g. *Pycnoporellus fulgens* that tend to occur on wood decayed by *Fomitopsis pinicola* (Niemelä et al. 1995).

Mean numbers of species were significantly positively correlated with object diameter. However, these results probably partly reflect the larger areas, and indirectly volumes, sampled from large than from medium diameter trunks. The occurrences of five out of 27 individually analysed species were significantly related to diameter, two of them positively. There are few directly comparable studies related to substrate diameter. Renvall (1995) and Bader et al. (1995) report that individual species of red-listed and locally rare fungi favour relatively large logs. However, separating rare from common species, Kruys et al. (1999) found that, while rare species were positively associated with larger diameters, frequently occurring species generally had little or no preferences for certain diameter classes.

While there was no significant relation between number of species and sun-exposure, the occurrences of six individual species were significantly correlated to this variable. Somewhat contrary to our expectations, four of these preferred open rather than shaded habitats. Thus, cut wood left on site, especially logs, may support diverse fungal communities both in shaded stands and in open logging sites.

Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter (III).

Main questions addressed by the study:
1. How are densities of individual species affected by substrate exposure in a range from shaded to open conditions?
2. How are densities of individual beetle species influenced by diameter in a range from medium to large diameter substrates?

Enclosed four metre high stumps of spruce, birch, aspen and oak were monitored for six seasons. A total of 47 038 individuals of 316 saproxylic beetle species, including 40 red-listed species (Gärdenfors 2000), were collected. Eighty-five species including six red-listed species (a total of 35 237 individuals) were selected for species-specific analyses of densities of individuals in relation to substrate sun-exposure and diameter.

Forty-two species were significantly related to exposure in any of the categorised or linear models. Twenty-nine of these (69%) had higher densities in semi-/fully exposed conditions (exposure > 0.33), while 13 (30%) had higher densities in shade. Proportions calculated from density ratios for the full set of species in the analyses, including non-significant species, were fairly similar, 66% and 34%, respectively. These results have important implications for conservation and management, as semi- or fully exposed conditions normally arise through either natural or artificial disturbances.

A considerable majority of species that used aspen and oak as their main hosts preferred exposed conditions. However, spruce (and somewhat surprisingly birch) hosted fairly equal proportions of 'exposure-' and 'shade-species'.

Mean densities calculated separately for shaded, semi- and fully exposed conditions indicated that most 'shade-species' and 'sun-species' performed considerably better in their 'best' compared to 'second best' conditions. However, most species that attained their highest densities in semi-exposed conditions performed comparably well also in fully exposed conditions.

Half of all species in our analyses were not significantly affected by exposure, i.e. any such density differences fell below the threshold of detection. However, even if some species may be almost indifferent or neutral, such classifications are difficult to test as they rest on negative rather than positive evidence. For purposes of conservation and management, it seems more useful to consider all species as either (more or less) positively or (more or less) negatively affected by exposure. Similar arguments apply to diameter, or indeed any continuous habitat variable.

Twenty species were significantly correlated with stump diameter. Of these, twelve performed better in medium than in large diameter stumps, while eight showed the opposite pattern. Slopes of regression lines of all modelled species indicated that equal proportions were favoured by large and medium diameters, respectively. There were no major differences between the faunas of different main host trees.

There were no significant differences between group mean diameter and exposure calculated from means per individual and species, either between analysed (n=85) and non-analysed species (n=231), or between red-listed (n=40) and non red-listed species (n=276). This indicates that the proportions found in the analyses apply to a very large set of common and less common beetle species that utilise medium and large diameter stumps of spruce, birch, aspen and oak during early stages of decay. While our data derive from only one site, all but five analysed species are found over most of Sweden. Thus, proportions are unlikely to be much influenced by aberrant patterns in isolated or marginal populations, and the results are probably valid in a wider regional context.

Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles (IV).

Main questions addressed by the study:
1. How many species utilise the stumps and in what relative numbers of individuals?
2. How similar are the beetle faunas found in stumps of different tree species?
3. How are numbers of beetle species, and red-listed beetle species, influenced by tree species, diameter and sun-exposure?

A total of 86 690 individuals representing 527 species of saproxylic beetles were recorded from cut stumps and logs on the experimental plots during 1994-2001. The materials included 78 (15%) red-listed species. More than half of the sample, 47 038 individuals representing 316 species, including 40 (13%) red-listed species,

were trapped on enclosed 4-m stumps. Thus, these species had all to some extent utilised the stumps, for regeneration and/or for hibernation. All results in this study are based on data from this material.

The distribution of individuals varied by almost four orders of magnitude, from thousands of individuals of some bark beetles, to 64 species that were represented only by single individuals. The one hundred most numerous species had mean outputs that ranged from 0.3 to 278 individuals / stump of the main host tree species, and 'single best stump' outputs from three to more than 3000 individuals. Comparisons between numbers of exit holes and numbers of trapped individuals indicated that the traps generally detected less than half the total reproduction of most species. As expected, species that developed in the wood for two years (Ehnström and Axelsson 2002) were considerably more under-sampled than one-year species.

All tree species hosted different beetle communities. Spruce held the highest proportion of species confined to one host tree in the study, while oak had few such species. Generally, the faunas of deciduous trees were more similar to each other, with a maximum for birch-oak, than the faunas of any deciduous tree and spruce. Mean numbers of species per stump recorded 1995-2001 were fairly similar: spruce 28.9, birch 27.9, aspen 24.6 and oak 23.7 (adjusted for differences in diameters and exposures). Also, single average stumps of all tree species held similar proportions of the fauna found on a larger, standardised sample of the same host. Thus, stumps of all tree species were similarly 'efficient' in addressing their respective potential faunas.

Mean total numbers of red-listed species recorded 1995-2001 differed considerably between tree species. Aspen hosted 2.82, birch 1.41, spruce 1.22 and oak 0.77 red-listed species per stump (adjusted for differences in diameters and exposures). Significantly richer than the other tree species, the average aspen stump hosted more than twice as many red-listed species as spruce and birch, and almost four times more than stumps of oak. Expressed as means per stump, red-listed species constituted 12%, 5%, 4% and 2% of the faunas of spruce, birch, aspen and oak, respectively.

Patterns of utilisation over time differed between hosts of different tree species. Five seasons after cutting, mean annual numbers of species in stumps of deciduous trees had increased to fairly constant levels of 10-14 species a year. Spruce stumps however, hosted a rich fauna of mostly common species already the second and third season. Numbers of red-listed species on spruce, birch and aspen were initially low and reached their highest values by the end of the survey period. In contrast, aspen stumps hosted most red-listed species in the middle of the period. In 1997, red-listed species accounted for almost 20% of all species recorded from aspen, double the proportion found at any time from any other tree species.

Total numbers of species and red-listed species were significantly positively correlated with increasing stump diameter and exposure. However, with numbers per unit of mantle area as response variable, diameter became negatively significant for all species, and non-significant for red-listed species, indicating that

positive correlation was mainly an effect of larger sampling areas on larger diameter stumps.

Large (0.6m diameter) stumps were extrapolated to have hosted 1.60 – 1.81 times more species than medium (0.3 m) stumps. Numbers of species per area however, were only 0.69 – 0.75 times those extrapolated for medium stumps. Sun-exposed (0.79) stumps held 1.36 – 1.46 times more species than stumps in shade (0.19) regardless of response variable. Patterns for red-listed species were similar but differences were more pronounced, indicating that the red-listed fauna was more favoured by large diameters, and to a certain extent by sun-exposure, than species in general.

Beetles and fungi

While many saproxylic beetles are pioneers that either benefit from or tolerate more or less open conditions generated by stand level disturbances, numerous saproxylic fungi seem to prefer or tolerate more shaded habitats. Such differences are reflected in the early colonisation by beetles and fungi of high stumps (the only substrate that permitted comparisons for the full period):

(a) Numbers of species of fungi, as well as occurrences of common species, were little affected by sun-exposure (or factors correlated to this variable). Numbers of species of beetles however, were significantly positively related to exposure. So were occurrences of individual species; the densities of half of all modelled species were significantly correlated to exposure, some two thirds of these positively and one third negatively. In contrast, large diameter substrates were less important to beetles than to fungi.

(b) Beetle diversity increased relatively more rapidly (red-listed species lagged somewhat behind) than diversity of fungi (Fig. 1).

(c) Red-listed species constituted a considerable proportion (13%) of the beetles that utilised high stumps, while no red-listed fungi were recorded from such substrate 1995-2002. These differences are larger than would be expected if they accurately reflected the proportions of red-listed vs. non red-listed saproxylic species at a national level (38% beetles and 10% fungi, respectively; information from the Swedish Species Information Centre). These differences may result from standing wood being a generally more suitable habitat for beetles than for fungi, and/or as a consequence of beetles generally utilising wood in earlier stages of decay than fungi. Fig. 1 indicates that the latter hypothesis may explain at least some of the differences. If so, additional red-listed species of fungi may colonise the stumps as wood decay proceeds further.

Figure 1. Annual, cumulative species accumulation on four metre stumps expressed as percentages of the total number of species recorded for the full survey period 1995-2001 (no sampling was performed in 1999).
Saproxylic beetles (n=316), red-listed saproxylic beetles (n=40) and saproxylic fungi (n=91).
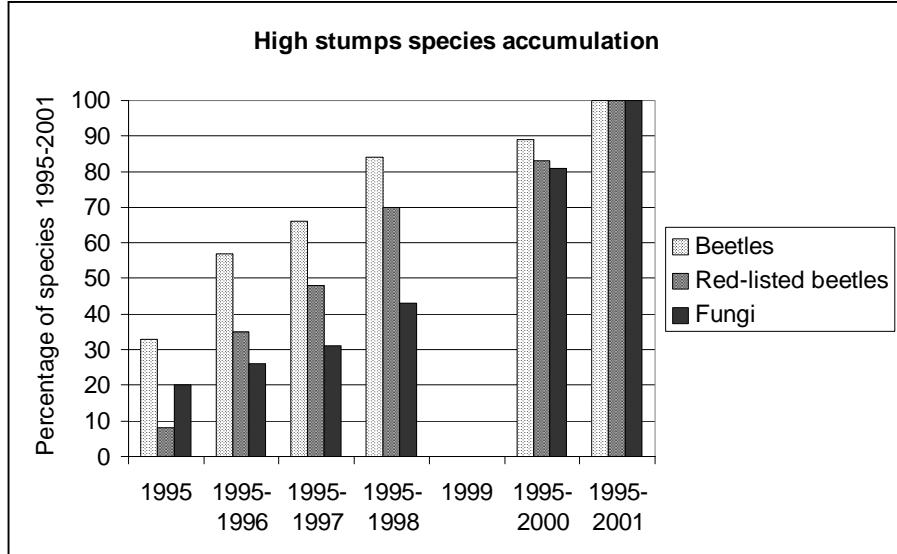
Implications for conservation

Cut wood as substrate for saproxylic organisms

Since this study was initiated, others have demonstrated that many species of saproxylic beetles are attracted to dead wood on clear-cuts (e.g. Ahnlund 1996; Martikainen 2001; Sverdrup-Thygeson and Ims 2002). Sieving has also shown that numerous beetles, including red-listed species, breed in such substrates (Jonsell and Weslien 2003; Jonsell et al. in press).

Our studies demonstrate that two thirds of the large beetle fauna that utilises dead trunks of spruce, birch, aspen and oak during earlier stages of decay favours substrates in semi- or fully exposed conditions. In Scandinavia, such substrates are normally associated with forest disturbances at the stand level (more stable, open forest types occur only in high altitudes or on dry rocky outcrops). Historically, large forest areas were affected by natural or antropogenic fires (Zackrisson 1977; Niklasson and Granström 2000; Niklasson and Drakenberg 2001). Such areas must have produced vast amounts of sun-exposed substrates (even if low intensity fires sometimes caused little tree mortality). Today, levels of dead wood are reduced by one order of magnitude compared to natural forest landscapes (Siitonen et al. 2001) and most mortality occurs in closed-canopy stands (Fridman and Walheim 2000). Thus, lack of suitably sun-exposed substrate may be an even more severe

problem for many saproxylic species than the generally low levels of dead wood in managed forests per se.

Sun-exposed substrates however, can also be generated by active measures. Our studies demonstrate that a substantial proportion of the saproxylic beetle fauna, including numerous red-listed species, can breed in 'artificially created' high stumps. We also show that such stumps are unlikely to generate dangerous levels of pest species. Unfortunately, conservation measures in managed forests are often perceived as inferior and of little value compared to reserves and set-aside areas. Far from all foresters and conservationists are aware that more or less all clear-cuts with retained high stumps and fallen trees host red-listed beetles, and that, in the absence of natural disturbances, logging is essential to create the open conditions necessary for many of these species. As a result, practises such as cutting high stumps, girdling trees, or felling trees to be left on the ground, have got far less attention than they deserve.

Our studies also show that cut dead wood, especially large diameter logs, can host a diverse flora of saproxylic fungi including a number of red-listed species, already in earlier stages of decay. This indicates that felling trees to be left at the site, although seldom if ever practised in Scandinavia today, may be a valuable method to increase the amount of substrate for saproxylic fungi (and probably other organisms), both in reserves and in managed forest landscapes.

However, it is hardly possible to 'manufacture' all kinds of dead wood utilised by saproxylic organisms. To certain extents, cut stumps and logs resemble vital trees that die swiftly due to fire, wind, inundation or snow-pressure, and cut wood can probably serve as substitute for much of the fauna and flora associated with such natural substrates. On the other hand, cut wood normally lacks e.g. scorching by fire, and comparisons also indicate that cut substrates may display less heterogeneity and variation than their natural counterparts (Jonsell et al. in press). Moreover, numerous saproxylic organisms favour dead wood from suppressed trees that are weakened by competition for long periods before they eventually die due to self-thinning. These trees are often, while still alive, infected by heart-rot fungi that can act as precursors for other fungi later in the succession. They also provide habitat for a specialised saproxylic fauna (Ehnström and Axelsson 2002). Such substrates are probably difficult to mimic by artificial measures in managed stands.

Thus, active creation of dead wood is not a substitute for forest reserves. On the contrary, active conservation measures in managed stands and setting aside reserves are complementary strategies that address two major subsets of forest organisms, species adapted to stand level disturbances on the one hand, and species that prefer more stable conditions on the other. So far however, species adapted to disturbances have received less attention from conservationists than organisms traditionally associated with reserves. Unless this bias is rectified, it will be difficult to design and optimise comprehensive conservation strategies adapted to various regions and landscapes.

18

Local and regional saproxylic beetle diversity

Seven years of intensive sampling yielded more than five hundred species of saproxylic beetles. These represent 60% of all (approximately 890) saproxylic beetles ever reported from the province of Uppland (an area of almost 13 000 km^2, spanning from boreal forests to grazed old oak parklands, with numerous 'hot-spots' visited by entomologists for more than a century). Yet, as we hardly detected *all* locally occurring saproxylic beetle species, and as some species earlier reported from the province may be extinct, Fagerön probably holds an even higher proportion of the extant regional fauna.

Conditions for this rich diversity probably reflect high site productivity, a variety of deciduous tree species in the canopy, substantial amounts of dead wood, and a geographical location that favours a mixture of boreal and more southern faunal elements. However, while such sites may be uncommon, they are far from unique, especially in the eastern part of the province. Recent inventories have also demonstrated that some other favourable areas both in (Eriksson 2002; Jonsell and Eriksson 2002) and outside the province (Nilsson 2001) host similarly diverse faunas.

Ultimately, site diversity reflects past and/or present patterns of faunal dispersal. Ecological theories (Southwood 1977), as well as some experimental data (Ranius and Hedin 2001), indicate that beetles associated with long-term stable habitats such as large hollow trees may be little inclined to disperse outside their immediate neighbourhood. Pioneer species associated with ephemeral substrates however, like bark beetles (Nilssen 1978; 1984) and fire-specialised flatbugs (Coulianos 1989) have been observed to move over large distances. Landscape characteristics, as well as former intensities of subsistence practises and early industrial land use, make it less likely that Fagerön and other similar sites hold relict concentrations of historically much more continuously distributed substrates. Rather, such habitats are likely either to be of relatively recent origin, or to have formed 'islands' in less suitable environments for a long time. In either case most species in their faunas must have been fairly mobile to get there. Such mobility is quite consistent with the adaptations to exposure and disturbances demonstrated in our study and in line with results of experimental landscape-scale studies of saproxylic beetles in Norwegian boreal forests (Økland et al. 1996). This interpretation, if correct, has important implications for conservation and management, as mobile species are likely to be adapted to continuity of substrates in a 'landscape' rather than 'site' scale.

It is worth to point out that very little of this remarkable local saproxylic beetle diversity is detectable during normal field visits (inspection of visitors to flowers and fungi, reasonable amounts of bark-peeling and sap wood cutting, inspection of galleries and exit-holes). Thus, unless combined with considerable trapping efforts, biological surveys are likely to severely underestimate numbers of locally occurring saproxylic beetles (Martikainen and Kouki 2003), compared to the diversity of sedentary organisms like fungi, mosses, lichens or plants.

Concluding remarks

In Sweden alone, more than 2000 forest-dependent species are red-listed and thus considered potentially or actually threatened (Gärdenfors 2000). To be able to preserve as much as possible of this diversity, we need to know how different species react to various forms of habitat modifications, land use and management. However, substantial data on habitat preferences and population biology are restricted to a very limited number of red-listed organisms. To acquire sophisticated information about the rest within a conservation timeframe of say, one or two human generations, is probably a task beyond current or expected research resources. So what are the options?

So far, a common approach has been to focus on in-depth case studies of relatively few species in order to understand not only how they interact with their surroundings, but also the mechanisms behind those interactions. Such focused approaches may be perfectly relevant in relation to conservation and management of single flagship-species or ecological key-species. However, the practise of generalising the results of such studies into higher order patterns or theories used to predict responses of non-studied species and systems, is more questionable.

For such 'vertically' derived generalisations to be valid, there must be a high degree of biological similarity between the species that 'generate the theory' and the species that are the 'targets of predictions'. This is probably often the case for fundamental physiological processes and evolutionary mechanisms at the individual level, also within very broadly defined taxa. However, it is not clear that such similarities extend to the complex ecological patterns and interactions that are relevant in contexts of conservation and management. In fact, the huge diversity and variability of life in itself, as well as the abundance of pairs of closely related species with widely different life history traits and habitat preferences, suggest that there may be little, rather than much, non-trivial commonality as a basis for higher order theory. If this is indeed the case, it may explain why, in spite of decades of intensive research, many ecological generalisations lack the necessary predictive power to be useful in applied conservation biology (Hansson 2003).

Are there other ways? I am convinced that conservation biology would benefit from a stronger focus on studies of multi-species assemblages and how large numbers of species respond to various – natural and anthropogenic – environmental factors. Such studies often involve massive sampling and time-consuming identification processes. Furthermore, many aspects are best addressed by long-term, large-scale experiments, and ideally data should be collected from several different localities. Thus, as research resources are limited, depth must be sacrificed in favour of breath. Our studies, focusing on practically relevant, simple outcomes (such as that most of the many saproxylic beetles addressed in these studies are favoured by exposed conditions associated with disturbances), exemplify such approaches.

Generalisations from such multi-species studies will be 'horizontal' rather than 'vertical' and of a proportional character. Assuming that the responses of a subset of species (fairly randomly) chosen from a larger, taxonomically, ecologically (or even arbitrary) defined group have been tested, the probability that a non-studied

group member will show a certain response can be predicted. The quality of such predictions will be functions of (a) the variability of responses, and (b) the proportion of the full group represented by the subset. As in any experimental approach, data from several sites are preferable. However, generalisations based on multi-species data from single experiments are probably less sensitive, both to the specific properties of the experimental area and to pure chance, than results from non-replicated studies of one or a few species. The reason is that multi-species studies already incorporate much inter-species random effects in terms of local habitat quality and position in relation to geographic range. Most such variation is likely to be multidirectional, cancelling extremes and stabilising conclusions.

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