**BIODIVERSITY RESEARCH**

# Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures

Melodie A. McGeoch[1]*, Martin Schroeder[2], Barbara Ekbom[2] and Stig Larsson[2]

[1]*Centre for Invasion Biology, Department of Conservation Ecology and Entomology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa,* [2]*Department of Entomology, Swedish University of Agricultural Sciences, PO Box 7044, SE-750 07 Uppsala, Sweden*

## ABSTRACT

Saproxylic beetles constitute a significant proportion of boreal forest biodiversity. However, the long history of timber production in Fennoscandia has significantly reduced the availability of dead wood and is considered a threat to the conservation of saproxylic beetle assemblages. Therefore, since the mid-1990s dead wood retention in harvested stands has formed an integral part of silvicultural practices. However, the contribution of this biodiversity-orientated management approach to conserving saproxylic beetle assemblages in boreal forest landscapes that include production forestry remains largely untested. We examined differences in resident saproxylic beetle assemblages among stands under different management in a boreal forest landscape in Central Sweden, and in particular stands managed according to new conservation-orientated practices. We also investigated the relationship between beetle diversity and forest stand characteristics. Bark of coarse woody debris (CWD) was sieved for beetles in old managed stands, unmanaged nature reserves, and set-aside areas, and clear-cut stands harvested according to certification guidelines [new forestry (NF) clear-cuts]. All stand types contributed significantly to the total diversity of beetles found. While stand size, position, and distance to nearest reserve were unimportant, both the quality and the quantity of CWD in stands contributed significantly to explaining beetle abundance and species richness. This extends the previous findings for red-listed invertebrates, and shows that heterogeneous substrate quality and a range of management practices are necessary to maintain saproxylic beetle diversity in boreal forest landscapes that include production forestry. The unique abiotic conditions in combination with the abundant and varied CWD associated with NF clear-cuts form an important component of forest stand heterogeneity for saproxylic beetles. It is thus essential that sufficient, diverse, CWD is retained in managed boreal landscapes to ensure the conservation of boreal saproxylic beetle assemblages.

*Correspondence: Melodie McGeoch, Centre for Invasion Biology, Department of Conservation Ecology and Entomology, University of Stellenbosch, Private Bag X1, Matieland, South Africa. E-mail: mcgeoch@sun.ac.za*

## INTRODUCTION

Commercial logging of the boreal forest has been practised in most parts of Fennoscandia for at least 100 years, and in the southern parts of the region for over 200 years. This practice clearly has negative consequences for biodiversity, and an estimated 400 saproxylic beetle species are considered threatened as a direct result of timber production (Jonsell *et al.*, 1998). Modern, large-scale forestry results in habitat loss, fragmentation, and homogenization (Kouki *et al.*, 2001). The consequent reduction in the size and quantity of old and dead trees, logs, and stumps is

considered the primary mechanism causing an increase in the extinction risk of saproxylic taxa (Fridman & Walheim, 2000; Grove, 2002; Punttila *et al.*, 2004). The degree to which biological communities have been influenced by this long history of intensive forestry in the region is largely unknown, although approximately 2000 species of invertebrates and lower plants are threatened or near-threatened (red-listed) in Swedish boreal habitats (Gärdenfors, 2000). Concern about the impact of extensive and intensive logging on the biodiversity of the boreal forest, that had been escalating since the early 1970s, led to the rapid integration of conservation measures into silviculture practices in Fennoscandia

in the mid-1990s (Larsson & Danell, 2001). As a consequence, over the last decade there has been considerable focus on developing methods to maintain and restore biodiversity in commercially managed boreal forests (Ranius & Kindvall, 2004).

The approach to forest management aimed at maintaining biodiversity in boreal forests is twofold, including a change in management practices within logged patches (or stands) of forest, as well as consideration of the forest landscape (Angelstam & Andersson, 2001). Key physical structures that contribute to biodiversity have been identified and management practices designed to enhance them have been developed (Ranius & Kindvall, 2004). These include landscape and forest stand elements such as old-growth stands, coarse woody debris (CWD), large patches of deciduous trees, burnt forest, and buffer zones along streams (Larsson & Danell, 2001). The certification criteria currently in use therefore require actions to preserve and actively restore these elements in the landscape (Anonymous, 2000). As a consequence, most boreal forest landscapes consist of a range of stands of different ages and past and current management practices.

Although substantial evidence exists for the negative impacts of commercial forestry on saproxylic species diversity, largely via a decline in the quantity and heterogeneity of CWD, the overall efficacy of the biodiversity-orientated management practices remains largely untested (Niemelä, 1997; Simberloff, 2001). The practices were developed based on the assumption that the provision of more CWD would contribute positively to saproxylic species and assemblage conservation. Live tree retention on otherwise clear-cut stands and the retention of some fallen trees, stumps, and dead wood in such stands are included in biodiversity-orientated management (Larsson et al., 2006). While these 'new forestry' (NF) practices have now been implemented for over a decade, the contribution that NF clear-cut stands make to the diversity of saproxylic species in the landscape, has been little examined [although the value of stand components has been evaluated, e.g. high stumps (Lindhe & Lindelöw, 2004)]. Clearly, stand types represent different successional stages, providing different resource qualities and quantities, as well as different microclimates (Økland et al., 1996). Indeed, the contribution of forest stand heterogeneity, or the relative contributions of stands with different recent management histories, to total saproxylic diversity requires further examination (Edman et al., 2004; Gibb et al., 2006). Focus on only selected species, such as indicator or red-listed species, is likely to result in inadequate conservation of the full assemblage (Puumalainen et al., 2003; Juutinen & Mönkkönen, 2004). Moreover, the majority of studies to date have examined fine-scale associations between species and individual dead wood components within forest stands (Jonsson et al., 2005). The sampling methods that have been used may also have limitations; most studies of saproxylic beetle diversity patterns to date have used flight intercept, or window, traps (e.g. Kaila et al., 1997; Similä et al., 2002a). With this trap type, however, it is not possible to determine whether or not the species caught are actually resident and using the resource in question (Wikars et al., 2005). Therefore, a more focused evaluation of the response of saproxylic beetle assemblages associated with stands with different management and qualities is required.

In this study, we examined saproxylic beetle assemblages in a model boreal forest landscape in central Sweden. Our objectives were (1) to determine if saproxylic beetle diversity and assemblage structure differs in forest stands under different forms of current management, and in particular to compare the assemblage supported by clear-cut stands under new, conservation-orientated forestry management with other stand types, and (2) to quantify the relationship between beetle diversity and forest stand characteristics (resource quality and quantity, stand size, relative position, and distance to nearest reserve). We used a direct sample method, i.e. sieving of bark collected from CWD objects, and therefore our study concerns the subset of beetle species directly associated with CWD bark. This study is thus unique as it (1) uses a direct sampling technique to quantify saproxylic beetle diversity patterns and (2) then uses these data along with stand characteristics to identify important determinants of saproxylic beetle diversity (richness, abundance, and assemblage composition) in the landscape.

## METHODS

### Study landscape and stand selection

The study was conducted in central Sweden in the province of Hälsingland close to Delsbo (62° N, 16° E). One large block of land (hereafter denoted landscape) owned by the timber company Holmen Skog AB (www.holmen.com) was used for the study. The size of the landscape is 24 449 ha, of which 20 294 ha consist of forest land. The landscape is typical of the south-boreal region with Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies L. Karst.) as the dominant tree species. Birch (Betula pendula Roth., Betula pubescens Ehrh.) and aspen (Populus tremula L.) are the most common deciduous tree species, but they rarely constitute more than a small proportion in managed forest stands. Holmen Skog AB is certified according to FSC (Forest Stewardship Council, see www.fsc-sweden.org) and their land has been managed using silviculture methods developed for preservation and restoration of biodiversity for about 10 years. These practices include the creation of high stumps and green tree retention at final cuttings. In the study landscape, high stumps (3–5 m high stumps left during clearing) were systematically introduced in about 1995, and are presently at a density of 1.2 stumps per hectare (Schroeder et al., 2006).

A random sample of 65 stands was selected, with stand types interspersed across the landscape area, stratified based on stand age and management history (Ekbom et al., 2006). None of the sampled stands was isolated by physical barriers (e.g. fences) of any kind or alternative land uses, and all stands bordered other, sometimes similar, stand types. Four stand categories were targeted for sampling: (1) NF clear-cut stands (666 ha) that were 3–7 years old (n = 19). These are clear-cuts on which, according to new forestry practices designed to promote biodiversity conservation, creation of high stumps and green tree retention is practised at final cutting. (2) Old managed stands, last logged = 60 years ago (5411 ha), where recruitment of new

CWD has begun (*n* = 23). (3) Set-aside stands (1920 ha) that have been excluded from management by the owners, but have no legal protection (*n* = 9). These are much smaller than reserve stands, but larger than old managed stands, and their designation by forestry companies is based on an undefined perception of their natural value as well as features that render them unsuitable for logging. (4) Reserve stands (751 ha), which are legally protected areas [*n* = 3 reserves (used in inference tests), but divided into 14 stands]. Although no silvicultural management has taken place recently in the last two stand categories, there was most likely some selective logging before these stands became protected 15–20 years ago.

### Sampling of coarse woody debris and beetles

Stands were surveyed to obtain an estimate of coarse woody debris (CWD) availability. Within each chosen stand, sampling of logs (downed woody debris) was carried out using four transects of 100 m in each stand (Marshall *et al.*, 2000; Ståhl *et al.*, 2001). The classification into decay classes was based on the hardness of the wood for all tree species (Renvall, 1995; Siitonen & Saaristo, 2000). Further details of the CWD sampling, bark volume, and bark area calculations for this landscape are outlined in Ekbom *et al.* (2006).

Beetles were sampled directly by bark sieving (Wikars *et al.*, 2005). Bark was peeled off and broken into small pieces that were sifted through a coarse net. The resulting fine fraction was placed in Tullgren funnels, where beetles were extracted under a lamp (Southwood & Henderson, 2000). To standardize the quality of bark sampled, beetles were sampled from early decay CWD, but excluding pieces dead for less than a year which are mostly colonized by bark beetles. CWD in the chosen decay classes (2 and 3, the wood is more than 1 year old and a knife can be pushed into the trunk 0–2.4 cm) was likely to still have bark. In total 10 CWD objects from separate piles of CWD were sampled in each stand. Objects were generally chosen from those found on transects or in plots delimited by transects (see Ekbom *et al.*, 2006). Standing and downed CWD of spruce, pine, and birch were sampled. If 10 objects were not found near the CWD sampling sites, the stand was searched for additional objects. In stands where 10 suitable objects were not available all appropriate objects were sampled. Sampled bark area per object ranged between 0.3 m$^2$ and 1 m$^2$ (where possible 1 m$^2$ was sampled, otherwise all available bark on the object was sampled). Tree species, diameter, and position (standing or downed) were recorded for each sampled object. All adult Coleoptera were identified to species or genus level. Only species known from previous studies to be saproxylic were included in the analyses (Dahlberg & Stokland, 2004).

### Analyses

Data within stands were pooled across the 10 sampled objects. Species richness and abundance in a stand therefore represented the total number of individuals and species sampled in that stand. Individual-based rarefaction curves were compiled for all stands and each stand type (EstimateS version 5, R.K. Colwell, http://viceroy.eeb.uconn.edu/estimates, see also Gotelli & Colwell, 2001). Rarefaction is advocated as the appropriate method to standardize data sets and allow for meaningful comparison of species richness between them (Gotelli & Colwell, 2001). In addition to individual-based curves, rarefaction curves were generated using the number of species against the total area (m$^2$) of sampled bark per stand (species density) rather than the number of individuals. Two species richness estimators (generally considered to be well performing; Walther & Moore, 2005; Hortal *et al.*, 2006) were used to evaluate sampling representivity, i.e. the Incidence Coverage Estimator (ICE) and Chao1 (Colwell & Coddington, 1994). When these estimators converge closely at the highest observed richness, then richness estimates may be considered representative (Longino *et al.*, 2002). Nonetheless, species richness estimators are often biased, and the use of multiple estimates may at best be considered to provide upper and lower bounds for richness estimates (Brose *et al.*, 2003; O'Hara, 2005). The number of species shared between stand types was also estimated using the Chao Estimator (Chao *et al.*, 2005), and the program SPADE on abundance data (Chao & Shen, 2003–05), that reduces undersampling bias and is particularly appropriate in data sets with many rare species (Chao *et al.*, 2005). Singletons were included in all analyses in this study, because the sampling approach used minimized the chance of sampling 'tourists' (species that do not use the resource being sampled, Gaston, 1994) and the species considered are known from previous studies as bark-associated saproxylics (Jonsell *et al.*, 1998; Magurran, 2004). All species analysed were therefore considered to be a resident component of the saproxylic beetle assemblage (although not all are necessarily exclusively saproxylic).

Because resource availability is known to affect saproxylic species richness (S) and abundance (N) (Martikainen *et al.*, 2000), this relationship was examined using several measures of resource availability per stand [both sampled and available bark area (m$^2$), volume of dead wood (m$^3$), lying vs. standing wood, as well as quantity of bark of pine, birch and spruce, and mean size (m$^3$) of CWD objects in the stand]. Sampled bark area was always included as a covariate in explanatory generalized linear models to accommodate unequal sample effort (bark area available differed between objects and stands) between stands. Other potential explanatory environmental variables considered included distance to nearest reserve (km) and stand area (ha). Data across stands within each of the three reserves were pooled to avoid pseudoreplication. Generalized linear models of abundance and species richness counts were constructed, assuming Poisson error distributions and using a logarithmic link function (McCullagh & Nelder, 1989). Goodness of fit was measured using the deviance statistic, and the proportion of explained deviance was calculated for each model. Because the study was spatially explicit, third-order polynomial generalized linear model analysis of the position of each stand (latitude and longitude coordinates) on richness (S) and abundance (N) was conducted (following Legendre & Legendre, 1998; see also McGeoch & Price, 2004). Resulting significant locational terms were then included in models with explanatory environmental variables.

Best-fit model selection (using the Akaike information criterion) was used to identify the explanatory environmental variables to be included in the final models (Dobson, 2002). Three sets of models were run for each dependent variable (N and S). These were (1) considering measures of total sampled and available wood resource, (2) total resource separated into lying and standing objects, and (3) total resource separated into the three host tree species (the deciduous category included predominantly birch, and only birch bark was sampled in this category).

Multivariate analysis was used to identify species associated with different stand types and to compare relative differences in assemblage structure among stand types. The weighted averaging, unimodal ordination method, Canonical Correspondence Analysis (CCA), was conducted using CANOCO 4.5 (Ter Braak & Smilauer, 2002) on log-transformed data. This choice was based on an examination of gradient lengths following Detrended Correspondence Analysis (Leps & Smilauer, 2003). The null hypothesis of independence between corresponding rows and columns of the species data matrix was tested using Monte Carlo permutation tests (Leps & Smilauer, 2003). Beetle assemblage structure between stand types was also compared using Analysis of Similarity (ANOSIM) based on group averaging and Bray–Curtis similarity measures (Clarke & Warwick, 1994). Abundance data were forth root transformed prior to analysis to weight common and rare species equally (Clarke & Warwick, 1994).

## RESULTS

### Species richness

A total of 184 species and 10 646 adult saproxylic beetle individuals were sampled across stands (see Appendix S1 in Supplementary Material). Approximately 50% of the species were represented by fewer than five individuals, 19% of species were singletons, and only 18 species were found in all stand types. One single genus (*Crypturgus* spp.; possibly four species) represented 38% of all individuals sampled, with the next two most abundant species constituting only 7% of the total number of individuals each.

Rarefaction curves did not asymptote for either all stands sampled or each stand type (Fig. 1), demonstrating that greater sample effort is required to represent the full species complement of saproxylic beetles in this area. However, individual-based rarefaction curves suggest that reserves, followed by NF clear-cut stands are likely to have higher species richness than set-aside or old managed stands (Fig. 1). By contrast, bark area rarefaction curves were very similar for all stand types, although the reserve stand curve had a somewhat more rapid accumulation of species per unit bark area (Fig. 1).

Species richness estimates for the total area (i.e. across all stands) ranged between 207.92 ± 13.09 (Chao1) and 227.42 ± 0.02 (ICE). Estimated richness for the individual stand types was higher than observed richness in all cases by between approximately 11 and 55 species (Table 1). The range of these richness estimators suggests that reserves and old managed stands are likely to have higher species richness than set-aside or NF clear-cut stands (Table 1).

## Stand characteristic effects on abundance and richness

There was some variation in sampled and available wood resource among stand categories (see Appendix S2 in Supplementary Material). For example, a higher amount of standing bark area was sampled in reserves and set-asides than in the other stand types, reflecting the higher proportion of available standing bark area in these categories (Appendix S2). Available deciduous bark (predominantly birch) was also higher in reserves and set-asides than in old managed or NF clear-cut stands. The proportion of pine bark sampled was also highest in reserves and lowest in NF clear-cuts. Bark area available also differed among stand types, with more bark area available in reserves than in NF clear-cuts (Appendix S2).

The spatial position of stands, stand area, distance to a nature reserve, or measures of CWD volume did not contribute significantly to explaining beetle abundance or richness, and did not enter into final explanatory models. More than 60% of the deviance in beetle abundance was explained by the final explanatory models that included predominantly resource variables (A1–A3, Table 2). The area of bark available and stand type contributed significantly and positively to all three abundance models (Table 2). The relationship between bark area available (BA) and beetle abundance (N) was also examined for the subset of stands where the quantity of bark area sampled was the same (10 m$^2$, $n = 25$, including stands of all types). The relationship remained significantly positive (d.f. = 23, scaled deviance/d.f. = 0.89, deviance explained = 36.75%, $\chi^2 (1) = 13.93$, $P < 0.002$, $N = 4.91 + 0.002*BA$). Beetle abundance predicted from model 3 (Table 2, highest percentage deviance explained for the three models) was significantly higher in set-aside and old managed stands than it was in NF clear-cuts (Table 1). The effect of bark area on beetle abundance was largely attributable to lying rather than standing bark area sampled (Table 2, model 2). The quantity of spruce bark sampled and available spruce and pine bark also contributed significantly to explaining beetle abundance, whereas other tree species-related variables did not (Table 2, model 3). Because the beetle assemblage was disproportionately dominated by *Crypturgus*, and this may mask potentially explanatory relationships, the above abundance models were repeated for *Crypturgus* abundance on its own, and total abundance excluding *Crypturgus* individuals (Table 3). The abundance of this dominant group was positively and significantly related to available bark area, the area of sampled lying and spruce bark area, and available deciduous bark area (Table 3). The abundance of this species was also significantly lower in NF clear-cut stands than other stand types. The abundance of non-*Crypturgus* beetles was significantly, positively related to standing bark area sampled, as well as to available bark area of lying wood and spruce bark (Table 3). Abundances excluding *Crypturgus* were also higher in set-aside and old managed than in NF clear-cut stands (Table 3).

Between 63% and 70% of the deviance in species richness was explained by the final explanatory models (B1–B3, Table 2). The area of sampled bark (measured in total or divided into position or tree species) was the only variable that contributed
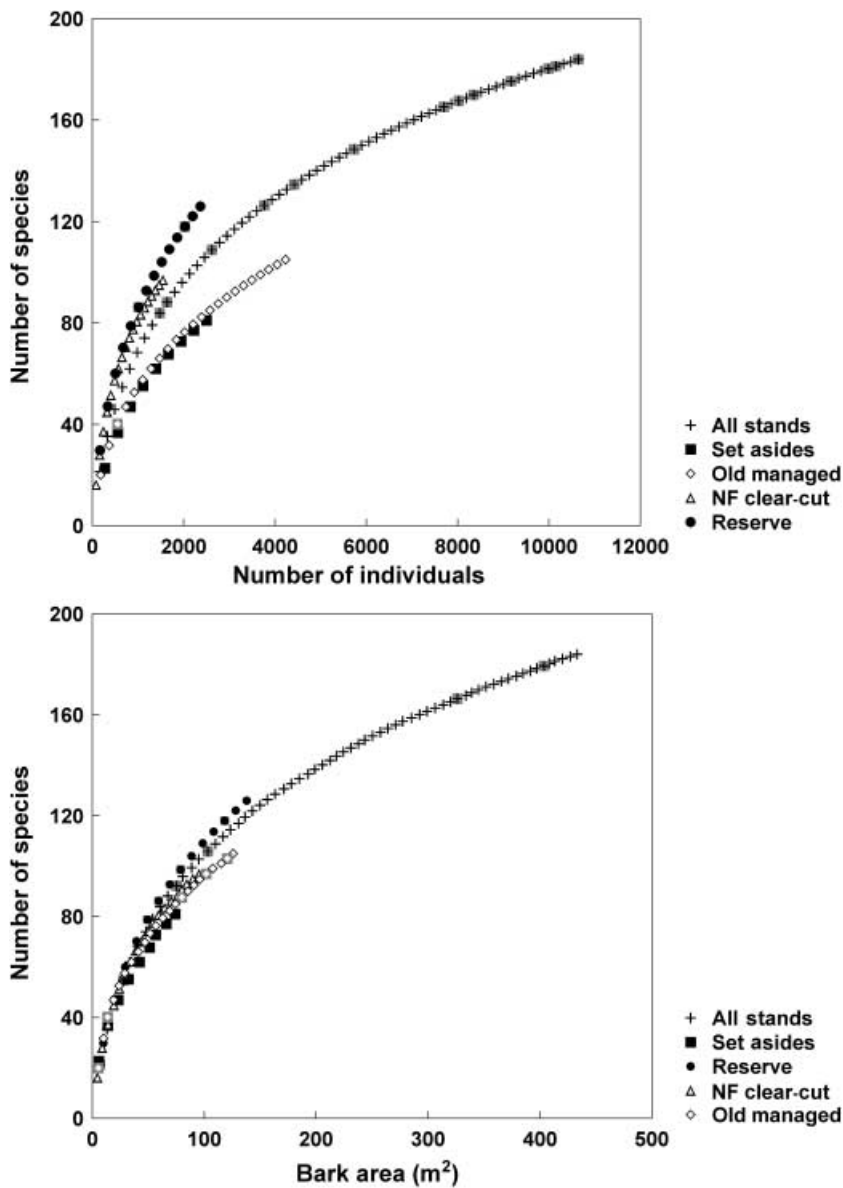
Figure 1 Individual-based (above) and sampled bark area-based (below) rarefaction curves for species sampled across all stands and in each stand type.

Table 1 Saproxylic beetle diversity in boreal forest stand types. S, species richness; N, number of sampled individuals; No St., number of sampled stands; ES, richness estimates in brackets provided by ICE and Chao1 (see Methods); $S_{RL}$ = number of red listed species; NF, new forestry. †Generalized linear model results provided in Table 2. Predicted means for reserves (*) were based on $n = 3$.

| Stand type | No St. | S (ES) | $S_{RL}$ | Species per stand (mean ± SE) | Predicted means† (mean ± SE) |
|---|---|---|---|---|---|
| Reserve | 14 (3*) | 127 (166.71 ± 4.63; 138.95 ± 8.73) | 11 | 29.57 ± 1.66 | 21.82 ± 0.34a* |
| Set-aside | 9 | 81 (119.07 ± 6.27; 105.19 ± 14.7) | 5 | 22.78 ± 2.82 | 26.01 ± 0.13a |
| Old managed | 23 | 105 (160.21 ± 0.13; 121.14 ± 12.68) | 5 | 20.04 ± 1.77 | 22.16 ± 0.08a |
| NF clear-cut | 19 | 97 (110.26 ± 1.9; 137.28 ± 0.06) | 8 | 16.26 ± 1.84 | 15.16 ± 0.11b |
| | | *N* | | Individuals per stand (mean ± SE) | |
| Reserve | 14 (3*) | 2366 | | 169.07 ± 22.79 | 209.38 ± 0.59ab* |
| Set-aside | 9 | 2502 | | 278.00 ± 84.35 | 235.02 ± 0.20a |
| Old managed | 23 | 4233 | | 184.04 ± 33.29 | 180.21 ± 0.15a |
| NF clear-cut | 19 | 1545 | | 81.32 ± 14.08 | 80.03 ± 0.22b |

Table 2 Best fit explanatory generalized linear models for number of individuals and species of beetles associated with different stand types (reserve, set-aside, old managed, new forestry clear-cut). The three models use different measures of the area of bark sampled, i.e. total, and separated into tree position and tree species.

| | Goodness of fit | | | Likelihood type III test | | |
|---|---|---|---|---|---|---|
| Abundance | d.f. | Scaled deviance | % DE | Independent variable/factor (sign of estimate) | $\chi^2$ (d.f.) | $P<$ |
| A1. Total bark area sampled | 46 | 47.80 | 60.03 | Area bark sampled, $m^2$ (−) | 0.14 (1) | ns |
| | | | | Total bark area available (+) | 7.21 (1) | 0.01 |
| | | | | $x$ | 0.02 (1) | ns |
| | | | | $y^3$ | 0.02 (1) | ns |
| | | | | Stand type | 10.33 (3) | 0.05 |
| A2. Bark area from lying and standing trees | 46 | 46.0 | 65.50 | Area sampled lying, $m^2$ (+) | 3.91 (1) | 0.05 |
| | | | | Area sampled standing, $m^2$ (+) | 0.01 (1) | ns |
| | | | | Total lying bark area, $m^2$ (+) | 7.12 (1) | 0.01 |
| | | | | Total standing bark area, $m^2$ (−) | 0.13 (1) | ns |
| | | | | Stand type | 12.53 (3) | 0.01 |
| A3. Birch, pine, and spruce bark area | 44 | 43.70 | 72.56 | Area sampled birch, $m^2$ (+) | 0.81 (1) | ns |
| | | | | Area sampled pine, $m^2$ (−) | 0.53 (1) | ns |
| | | | | Area sampled spruce, $m^2$ (+) | 7.73 (1) | 0.01 |
| | | | | Total deciduous area available (+) | 2.09 (1) | ns |
| | | | | Total pine area available (−) | 4.08 (1) | 0.05 |
| | | | | Total spruce area available (+) | 3.49 (1) | 0.06 |
| | | | | Stand type* | 17.27 (3) | 0.001 |
| Species richness | | | | | | |
| B1. Total bark area sampled | 46 | 55.42 | 63.16 | Area bark sampled, $m^2$ (+) | 3.09 (1) | 0.07 |
| | | | | $x^2y$ | 1.04 (1) | ns |
| | | | | $x^3$ | 1.09 (1) | ns |
| | | | | Total bark area available | 0.15 (1) | ns |
| | | | | Stand type | 4.02 (3) | ns |
| B2. Bark area from lying and standing trees | 46 | 51.70 | 69.57 | Area sampled lying, $m^2$ (+) | 5.83 (1) | 0.01 |
| | | | | Area sampled standing (+) | 8.61 (1) | 0.001 |
| | | | | Total bark area lying, $m^2$ (+) | 8.07 (1) | 0.01 |
| | | | | Total bark area standing, $m^2$ (−) | 8.10 (1) | 0.01 |
| | | | | Stand type* | 10.39 (3) | 0.01 |
| B3. Birch, pine, and spruce bark area | 44 | 52.11 | 65.55 | Area sampled birch, $m^2$ (+) | 1.28 (1) | ns |
| | | | | Area sampled pine, $m^2$ (+) | 0.27 (1) | ns |
| | | | | Area sampled spruce, $m^2$ (+) | 4.63 (1) | 0.05 |
| | | | | Total deciduous area available (+) | 0.24 (1) | ns |
| | | | | Total pine area available (+) | 0.63 (1) | ns |
| | | | | Total spruce area available (+) | 0.58 (1) | ns |
| | | | | Stand type | 3.90 (3) | ns |

DE, deviance explained; *Predicted means provided in Table 1.

consistently to explaining species richness (Table 2). However, available bark area of both standing and lying trees also contributed significantly to explaining species richness (Table 2, model B2). Only the area of sampled spruce bark was significant in model B3 (Table 2). The relationship between species richness and total bark area available, as before using only the subset of stands in which an equivalent amount of bark area was sampled, was not significant ($\chi^2$ (1) = 1.62, $P$ = 0.20). Stand type contributed significantly in only one of the three models (Table 2), and in this case there were significantly fewer species in NF clear-cut stands than in all other stand types (predicted means in Table 1).

**Beetle assemblage composition**

Stands types were estimated to share 50−67% of species (Table 4). Reserves were estimated to share the most species with old managed and set-aside stands, and the least species were shared by reserve and NF clear-cut stands (Table 4). The number of species found in only one stand type was highest for reserves (28) and NF clear-cuts (22) (Table 4). There were significant differences in beetle assemblage structure between stand types (Global R = 0.515, $P$ < 0.001, Table 4). While reserve and set-aside stand assemblages were not significantly different, the assemblages associated with all other stand types were (Table 4).

**Table 3** Best fit explanatory generalized linear models for the abundance of *Crypturgus* spp. and total beetle abundance excluding this species. Stand types: reserve (R), set-aside (SA), old managed (OM), new forestry clear-cut (NF). The three models use different measures of the area of bark sampled, i.e. total, and separated into tree position and tree species.

| *Crypturgus* sp. abundance | Goodness of fit | | | Likelihood type III test | | |
|---|---|---|---|---|---|---|
| | d.f. | Scaled deviance | % DE | Independent variable/factor (sign of estimate) | $\chi^2$ (d.f.) | $P <$ |
| 1. Total bark area sampled | 48 | 45.86 | 44.47 | Area bark sampled, $m^2$ (+) | 0.03 (1) | ns |
| | | | | Total bark area available (+) | 8.87 (1) | 0.01 |
| | | | | Stand type | 13.43 (3) | 0.01 |
| 2. Bark area from lying and standing trees | 46 | 39.80 | 60.48 | Area sampled lying, $m^2$ (+) | 9.94 (1) | 0.01 |
| | | | | Area sampled standing, $m^2$ (−) | 0.49 (1) | ns |
| | | | | Total lying bark area, $m^2$ (+) | 2.95 (1) | ns |
| | | | | Total standing bark area, $m^2$ (+) | 0.01 (1) | ns |
| | | | | Stand type | 8.42 (3) | 0.05 |
| 3. Birch, pine, and spruce bark area | 44 | 32.80 | 65.54 | Area sampled birch, $m^2$ (+) | 1.83 (1) | ns |
| | | | | Area sampled pine, $m^2$ (−) | 0.44 (1) | ns |
| | | | | Area sampled spruce, $m^2$ (+) | 7.11 (1) | 0.01 |
| | | | | Total deciduous area available (+) | 3.65 (1) | 0.05 |
| | | | | Total pine area available (−) | 3.40 (1) | 0.06 |
| | | | | Total spruce area available (+) | 0.42 (1) | ns |
| | | | | Stand type* | 13.55 (3) | 0.01 |
| **Abundance excluding *Crypturgus* sp.** | | | | | | |
| 1. Total bark area sampled | 48 | 46.98 | 66.45 | Area bark sampled, $m^2$ (+) | 0.14 (1) | ns |
| | | | | Total bark area available (+) | 1.67 (1) | ns |
| | | | | Stand type | 8.22 (3) | 0.05 |
| 2. Bark area from lying and standing trees | 46 | 43.30 | 69.12 | Area sampled lying, $m^2$ (−) | 0.10 (1) | ns |
| | | | | Area sampled standing (+) | 3.10 (1) | 0.07 |
| | | | | Total bark area lying, $m^2$ (+) | 4.69 (1) | 0.05 |
| | | | | Total bark area standing, $m^2$ (−) | 0.52 (1) | ns |
| | | | | Stand type | 11.29 (3) | 0.05 |
| 3. Birch, pine, and spruce bark area | 44 | 40.80 | 74.01 | Area sampled birch, $m^2$ (−) | 0.05 (1) | ns |
| | | | | Area sampled pine, $m^2$ (+) | 0.91 (1) | ns |
| | | | | Area sampled spruce, $m^2$ (+) | 6.34 (1) | 0.05 |
| | | | | Total deciduous area available (−) | 0.22 (1) | ns |
| | | | | Total pine area available (−) | 2.13 (1) | ns |
| | | | | Total spruce area available (+) | 3.09 (1) | 0.07 |
| | | | | Stand type† | 5.89 (3) | 0.05 |

DE, deviance explained; *R = [(SA = OM) > NF]; †[(SA = OM) > NF] = R.

**Table 4** Number and percentage of species shared between stand types. Observed species shared in lower left half of matrix with estimated shared species (± SE with 95% CI in brackets below) in upper right (Chao shared species estimator, Chao *et al.*, 2005). Multivariate Analysis of Similarity results in square brackets in lower left [Global R-value (that lies between 0 and 1), * = significant at $P < 0.001$].

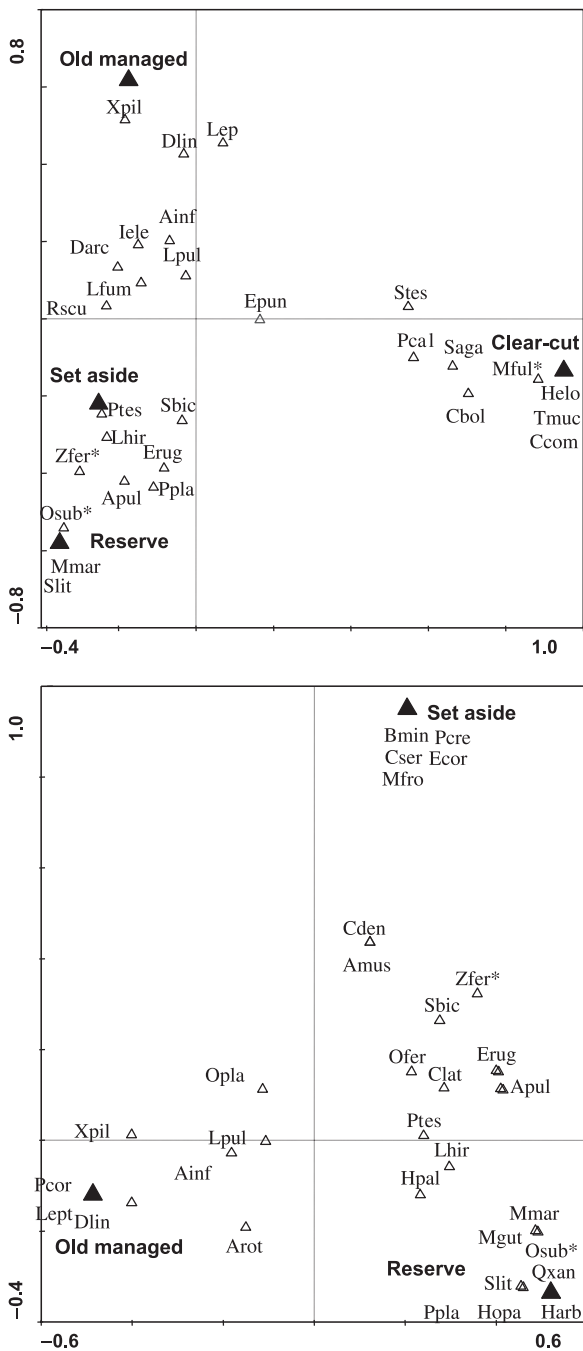| Stand type (no. of unique species) | Reserve | Old managed | Set-aside | NF clear-cut |
|---|---|---|---|---|
| Reserve (28) | | 102.67 ± 14.1 | 85.89 ± 12.3 | 78.24 ± 10.5 |
| | | (82.0, 133.5) | (68.3, 115.2) | (67.0, 100.8) |
| | | 67.10% | 61.79% | 50.15% |
| Old managed (17) | 78 | | 74.38 ± 10.5 | 77.47 ± 11.2 |
| | 50.98% | | (59.0, 95.9) | (65.0, 101.8) |
| | [R = 0.85*] | | 58.56% | 56.55% |
| Set-aside (9) | 68 | 59 | | 65.58 ± 11.4 |
| | 48.92% | 46.45% | | (52.0, 90.8) |
| | [R = 0.05ns] | [R = 0.86*] | | 61.87% |
| New forestry (NF) clear-cut (22) | 67 | 65 | 52 | |
| | 42.95% | 47.44% | 49.06% | |
| | [R = 0.58*] | [R = 0.21*] | [R = 0.49*] | |

**Figure 2** Canonical Correspondence Analysis correlation biplots (focus on species distances using biplot scaling and log-transformed data; species fit range > 10%) of all stand types (above) and excluding new forestry clear-cut stands (below). Centroids represent the four stand types and species abbreviations (first letter of genus followed by first three letters of species name, refer to Appendix S1 for species list). The distances between stand type centroids and species positions show the relative total abundances of the species in different stand types, i.e. the closer a species is to a particular stand type centroid, the higher its relative abundance is in that stand type. Distances between stand type centroids themselves represent the average chi-squared distances between the samples of the stand types being compared. *Red-listed species (Appendix S1). Species abbreviations provided in Appendix S1.

In the CCA ordination considering all stand types, the first two canonical axes explained 35.1% of the total variability, and stand type explained 43.0% of the variability in the species data (F-ratio = 1.48, P < 0.01) (Fig. 2). The NF clear-cut assemblage was well separated from the remaining stand types along the first CCA axis (explaining 20.5%), and several species were clearly associated with this stand type (Fig. 2). For clearer resolution of differences between the remaining three stand types, NF clear-cut stands were excluded and the analysis repeated. Here, the first two canonical axes explained 25.6% of the total variability, and stand type a similar 25.6% of the variability in species data (F-ratio = 1.34, P < 0.01). In this ordination, old managed stands were separated from reserve and set-aside stands along the first CCA axis (Fig. 2, explaining 16.9%). Again, several species were strongly associated with each stand type (i.e. species position on ordination close to stand type centroid) (Fig. 2).

## DISCUSSION

While 184 species were sampled in this study, 719 saproxylic beetle species are known from the province of Hälsingland (1260 species in Sweden) (Lundberg, 1995; Dahlberg & Stokland, 2004). However, considering only those species known to be associated with the tree species sampled in this study (as well as those for which no host association data are available), and excluding species living exclusively in live trees and inside fungal fruiting bodies, the estimated species pool for this study is 612 (Dahlberg & Stokland, 2004). Therefore, a conservative estimate of approximately 30% of the Hälsingland species pool was sampled in Delsbo, including 16% of the red-listed species (of a total of 98). This figure is reasonably high considering that the sampled landscape constitutes only 1.7% of the forest area in Hälsingland (National Board of Forestry, 2004). Nonetheless, rarefaction curves and richness estimates showed that additional sampling effort is likely to yield significantly more species in the study landscape. This is not an unusual outcome when sampling insect assemblages (Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Magurran, 2004; Chao et al., 2005; Jonsson et al., 2005), particularly when the assemblage comprises a high proportion of infrequent species as was the case here, and as is characteristic of saproxylic species (see also findings by Gibb et al., 2006). Although rare species are often locally abundant (Gaston, 1994), all the near-threatened and vulnerable species recorded in this study were found in very low abundances (with a maximum of 22 individuals for any of these species). Therefore, by virtue of their conservation status in Sweden and low abundance in this study, these species may be considered truly rare in the Delsbo landscape (Gaston, 1994).

## Saproxylic beetle diversity and forest stand management

The richness estimates for particular stand types were varied, and the only consistent outcome was the highest richness associated with reserve stands. In general, species richness associated with set-aside and old managed stands tended to be intermediate,

whereas NF clear-cut richness was lowest according to some estimators and higher than set-aside and old managed stands according to others. Results from related studies have been similarly variable. For example, saproxylic beetle species richness of old growth forests was significantly higher than that in old managed areas in one Finnish study (Martikainen *et al.*, 2000), but not in others (Similä *et al.*, 2002b, 2003). In both of the latter studies, however, richness was positively correlated with the diversity of dead wood. The results of our study thus do provide some support for the assumption that nature reserves, as a likely consequence of the greater quantity and more heterogeneous CWD substrate that they provide (as quantified for this landscape by Ekbom *et al.*, 2006), are generally host to a greater richness of saproxylic beetles than managed boreal forests.

Although richness differences among stand types were not straightforward to discern, abundance differences were marked; abundances were significantly higher in old managed and set-aside stands than NF clear-cuts. However, the beetle assemblage was disproportionately dominated by *Crypturgus* spp. and this dominance did, to some extent, mask abundance patterns in the remaining species [a related study focusing on early successional saproxylic beetles found 67% dominance by only two species, (Gibb *et al.*, 2006), suggesting that this is not unusual for these beetle assemblages]. For example, the individual-based rarefaction curves and the explanatory models reflect the lower species to individual ratios in old managed and set-aside stands, where *Crypturgus* spp. were significantly more abundant. By contrast, beetle abundances excluding *Crypturgus* spp. were significantly higher in old managed and set-aside than in NF clear-cut stands. Because species richness has a generally positive relationship with abundance (although in the presence of highly dominant species, such as *Crypturgus*, the slope of the relationship may be comparatively shallow) (Magurran, 2004), stands that support greater numbers of individuals are also generally likely to support more species.

While richness and abundance are the most commonly used measures of diversity, species identity and assemblage structure are often more informative measures of patterns of biodiversity (McGeoch *et al.*, 2002; Magurran, 2004). Although species richness estimate differences between stand types were not marked, the dissimilarity in assemblage structure strongly suggests that habitat heterogeneity, in addition to resource quantity, is important for maintaining saproxylic beetle diversity across the landscape. Similar conclusions have been reported when comparing old growth forest beetle assemblages with early succession (Similä *et al.*, 2002b) and clear-cut (Sippola *et al.*, 2002) beetle species assemblages. The latter studies were based on the collection of flying insects in window traps, and the results of the direct sampling approach reported here demonstrate that this pattern is generated by a resident fauna.

The comparatively high species richness and significantly different beetle assemblage structure associated with NF clear-cut stands demonstrate that these stands do contribute to total saproxylic beetle diversity in the landscape. Although clear-cutting is not optimal for biodiversity conservation, in forestry production landscapes these NF clear-cut stands may provide suitable habitat for an array of species not suitably accommodated in other stand types. Seven species were found to be clearly associated with NF clear-cuts in the ordination including all stand types (some of these known to be sun-loving, see Appendix S1). For example, *Hadreule elongatula*, one of the species found strongly associated with NF clear cuts stands in this study is known to be found virtually exclusively in forest gaps (Schroeder *et al.*, 2006). The prevalence of natural forest gaps, for example those created by fire, has decreased in managed forest landscapes because of fire control practices (Linder *et al.*, 1997). Clear-cut stands can thus provide suitable habitat for those species dependent on open habitat, such as gaps created by fire and storms, provided that sufficient suitable bark substrate is available (Ås, 1993). While traditional clear-cut stands provided similarly exposed patches prior to the introduction of conservation-orientated management approaches, the quantity of CWD on traditional clear-cuts was low (Ekbom *et al.*, 2006; Larsson *et al.*, 2006), and CWD was commonly destroyed at harvest (Siitonen, 2001; Hautala *et al.*, 2004). The combination of stand exposure and the availability and heterogeneity of CWD are thus responsible for the current conservation value of NF clear-cut stand in the Delsbo landscape. In this sense NF-clear cuts are more similar to clearings created by natural disturbances, such as insect and disease outbreaks, and windstorms, than traditional clear-cuts (Angelstam, 1997; Kuuluvainen, 2002). Therefore, as the results here show, in combination with later successional stage stands, NF clear-cuts may contribute positively to total biodiversity in forestry production landscapes.

## Saproxylic beetle diversity and stand characteristics

The finding that bark area sampled and bark area available were generally significant explanatory variables in models for richness and abundance is important in two respects. It confirms the validity of including this variable in models in order to examine the effects of other explanatory variables independently of the bark area effect. More importantly, however, because the quantity of bark area sampled across stands was constrained by bark area available, it supports the contention that a shortage of bark area in managed forest stands leads to a reduction in saproxylic beetle diversity in boreal forests (Grove, 2002; Punttila *et al.*, 2004).

Abundance models supported the importance not only of the quantity of bark area available, but also of a heterogeneous CWD resource, in maximizing saproxylic beetle diversity. Beetle abundances were generally higher in association with lying, rather than standing CWD, and in stands with greater quantities of available spruce bark [Norway spruce supports the most species-rich assemblage of wood-living species (Jonsson *et al.*, 2005)]. The species richness models also provided support for the importance of resource heterogeneity [CWD position (lying vs. standing) and tree species] in maintaining high species richness in boreal forest stands (see also Martikainen *et al.*, 2000; Jonsell & Weslien, 2003; Similä *et al.*, 2003). These findings thus validate the recommendation by Ekbom *et al.* (2006), based on an evaluation of CWD in this study landscape, that more spruce and deciduous wood should be left in Swedish boreal landscapes

during management. They also extend Jonsell *et al.*'s (1998) findings for red-listed invertebrates, i.e. that heterogeneous substrate quality and a range of management practices in production landscapes are necessary to maintain diversity, to boreal saproxylic beetle diversity in general.

Distance to closest reserve was not a significant explanatory variable for either beetles species richness or abundance. However, in the model landscape examined in this study, the maximum distance of any stand to the closest reserve was only 6 km. In other boreal forest landscapes, where managed forest stands are more isolated from the nearest protected areas, the effect of distance to reserve may well be more significant. Nonetheless, the absence of significant spatial structure (locality terms dropped out of the richness and abundance models) between forest stands suggests that local scale, within-stand characteristics are important determinants of saproxylic beetle diversity across the landscape, and that no strong environmental gradients are present across the landscape to which these beetles respond (Logerwell *et al.*, 1998; Bell, 2001; McGeoch & Price, 2004). Interestingly, Gibb *et al.* (2006) also found no relationship between site proximity and assemblage similarity in their study (conducted in northern Sweden) examining early successional beetle assemblages. Low species dispersal rates and a complex, heterogeneous matrix (high levels of within and between-stand habitat heterogeneity) combined with species with low densities and highly specialized resource requirements are the likely mechanisms that underlie the absence of spatial structure at the scale examined in this study (Ranta *et al.*, 1999; Schiegg, 2003; McGeoch & Price, 2004).

## CONCLUSIONS

This study demonstrates that forest stand heterogeneity, in the form of stands under different management and with sufficient quantity and diverse quality of resource substrates, is important for maintaining total resident saproxylic beetle diversity in production forestry landscapes. The heterogeneity of CWD substrate (both position and host tree species) contributes positively to local saproxylic beetle species richness. Furthermore, NF clear-cuts were shown to support a relatively diverse and in some ways unique (assemblage structure and habitat-specific species) beetle assemblage. Therefore, conservation-orientated management, by increasing the availability of suitable resources for saproxylic beetles, does contribute to the maintenance of total saproxylic biodiversity. It is therefore essential that both the quantity (particularly of spruce and deciduous wood) and the diversity of CWD are conscientiously upheld in production forestry landscapes to conserve this significant component of boreal forest biodiversity.

## ACKNOWLEDGEMENTS

## REFERENCES

Angelstam, P. (1997) Landscape analysis as a tool for the scientific management of biodiversity. *Ecological Bulletins*, **46**, 140–170.

Angelstam, P. & Andersson, L. (2001) Estimates of the needs for forest reserves in Sweden. *Scandinavian Journal of Forest Research Supplement*, **3**, 38–51.

Ås, S. (1993) Are habitat islands islands — woodliving beetles (Coleoptera) in deciduous forest fragments in Boreal forest. *Ecography*, **16**, 219–228.

Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413–2418.

Brose, U., Martinez, N.D. & Williams, R.J. (2003) Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, **84**, 2364–2377.

Chao, A. & Shen, T.-J. (2003–05) *Program SPADE (species prediction and diversity estimation)*. Program and User's Guide published at http://chao.stat.nthu.edu.tw.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.

Clarke, K.R. & Warwick, R.M. (1994) *Change in marine communities, an approach to statistical analysis and interpretation*. Natural Environmental Research Council, Swindon, UK.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **345**, 101–118.

Dahlberg, A. & Stokland, J. (2004) *Vedlevande arters krav på substraten sammanställning och analys av 3600 arter*. Skogsstyrelsen, Jönköping, Sweden.

Dobson, A.J. (2002) *An introduction to generalized linear models*, 2nd edn. Chapman & Hall/CRC Texts in Statistical Science, Boca Raton, Florida.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B.G. & Ericson, L. (2004) Spore deposition of wood-decaying fungi: importance of landscape composition. *Ecography*, **27**, 103–111.

Ekbom, B., Schroeder, L.M. & Larsson, S. (2006) Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. *Forest Ecology and Management*, **221**, 2–12.

Fridman, J. & Walheim, M. (2000) Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, **131**, 23–36.

Gärdenfors, U. (2000) *The 2000 red list of Swedish species*. Art-Databanken, SLU, Uppsala, Sweden.

Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.

Gibb, H., Hjältén, Ball, J.P., Atlegrim, O., Pettersson, R., Hilszczański, J., Johansson, T. & Danell, K. (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography*, **29**, 191–204.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. (2004) Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. *Biodiversity and Conservation*, **13**, 1541–1554.

Hortal, J., Borges, P.A.V. & Gaspar, C. (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology*, **75**, 274–287.

Jonsell, M. & Weslien, J. (2003) Felled or standing retained wood — it makes a difference for saproxylic beetles. *Forest Ecology and Management*, **175**, 425–435.

Jonsell, M., Weslien, J. & Ehnström, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, **7**, 749–764.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood — lessons for dead wood management. *Silva Fennica*, **39**, 289–309.

Juutinen, A. & Mönkkönen, M. (2004) Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. *Ecological Economics*, **50**, 35–48.

Kaila, L., Martikainen, P. & Punttila, P. (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbance in boreal forest. *Biodiversity and Conservation*, **6**, 1–18.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001) Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research Supplement*, **3**, 27–37.

Kuuluvainen, T. (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, **36**, 97–125.

Larsson, S. & Danell, K. (2001) Science and the management of boreal forest diversity. *Scandinavian Journal of Forest Research Supplement*, **3**, 5–9.

Larsson, S., Ekbom, B., Schroeder, L.M. & McGeoch, M.A. (2006) Saproxylic beetles in a Swedish Boreal forest landscape managed according to 'New Forestry'. *Insect biodiversity and dead wood. Proceedings of a Symposium for the 22nd International Congress of Entomology, Brisbane, Australia, 15–21 August 2004* (ed. by S.J. Grove and J.L. Hanula), pp. 75–82. General Technical Report. US *Department* of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.

Legendre, L. & Legendre, P. (1998) *Numerical ecology*. Elsevier, Amsterdam.

Leps, J. & Smilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.

Linder, P., Elfving, B. & Zackrisson, O. (1997) Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, **98**, 17–33.

Lindhe, A. & Lindelöw, Å. (2004) Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management*, **203**, 1–20.

Logerwell, E.A., Hewitt, R.P. & Demer, D.A. (1998) Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography*, **21**, 212–223.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology*, **83**, 689–702.

Lundberg, S. (1995) *Catalogus coleopterum sueciae*. Naturhistoriska Riksmuseet, Stockholm.

Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford.

Marshall, P.L., Davis, G. & LeMay, V.M. (2000) *Using line intersect sampling for coarse woody debris*. Forest Research Technical Report, Vancouver Forest Region, TR-003, Ecology. B.C. Ministry of FORESTS; Nanaimo, B.C., Canada.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, **94**, 199–209.

McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, London.

McGeoch, M.A. & Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, **73**, 506–516.

McGeoch, M.A., van Rensburg, B.J. & Botes, A. (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39, 661–672.

National Board of Forestry (2004) *Statistical yearbook of forestry 2004*. National Board of Forestry, Jönköping, Sweden.

Niemelä, J. (1997) Invertebrates and boreal forest management. *Conservation Biology*, **11**, 601–610.

O'Hara, R.B. (2005) Species richness estimators: how many species can dance on the head of a pin? *Journal of Animal Ecology*, **74**, 375–386.

Økland, B., Bakke, A., Havgar, S. & Torstein, K. (1996) What factors influence the diversity of saproxylic beetles? *European Journal of Entomology*, **93**, 195–209.

Punttila, P., Niemelä, P. & Karhu, K. (2004) The impact of wood ants on the structure of invertebrate community on mountain birch (*Betula pubescens* ssp. *czerepanovii*). *Annales Zoologici Fennici*, **41**, 429–446.

Puumalainen, J., Kennedy, P. & Folving, S. (2003) Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. *Journal of Environmental Management*, **67**, 5–14.

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.

Ranta, E., Kaitala, V. & Lindstrom, J. (1999) Spatially autocorrelated disturbances and patterns in population synchrony. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **266**, 1851–1856.

Renvall, P. (1995) Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, **35**, 1–51.

Schiegg, K. (2003) Environmental autocorrelation: curse or blessing? *Trends in Ecology & Evolution*, **18**, 212–214.

Schroeder, M., Ranius, T., Ekbom, B. & Larsson, S. (2006) Recruitment of saproxylic beetles in high stumps created for maintaining biodiversity in a boreal forest landscape. *Canadian Journal of Forestry Research*, **36**, 2168–2178.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscanian boreal forests as an example. *Ecological Bulletins*, **49**, 11–41.

Siitonen, J. & Saaristo, L. (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation*, **94**, 211–220.

Simberloff, D. (2001) Management of boreal forest — a view from outside. *Scandinavian Journal of Forest Research Supplement*, **3**, 105–118.

Similä, M., Kouki, J. & Martikainen, P. (2003) Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management*, **174**, 365–381.

Similä, M., Kouki, J., Mönkkönen, M. & Sippola, A.L. (2002a) Beetle species richness along the forest productivity gradient in northern Finland. *Ecography*, **25**, 42–52.

Similä, M., Kouki, J., Martikainen, P. & Uotila, A. (2002b) Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biological Conservation*, **106**, 19–27.

Sippola, A.L., Siitonen, J. & Punttila, P. (2002) Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. *Annales Zoologici Fennici*, **39**, 69–86.

Southwood, T.R.E. & Henderson, P.A. (2000) *Ecological methods*, 3rd edn. Blackwell Science, Oxford.

Ståhl, G., Ringvall, A. & Fridman, J. (2001) Assessment of coarse woody debris — a methodological overview. *Ecological Bulletins*, **49**, 57–70.

Swedish FSC Council (2000) *Svensk FSC-standard för certifiering av skogsbruk*. Svensk FSC-rådet, Uppsala, Sweden.

Ter Braak, C.J.F. & Smilauer, P. (2002) CANOCO *reference manual*. Wageningen University and Research Centre, Wageningen, the Netherlands.

Walther, B.A. & Moore, J.L. (2005) The concept of bias, precision, and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography*, **28**, 1–15.

Wikars, L.-O., Sahlin, E. & Ranius, T. (2005) A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Canadian Entomologist*, **137**, 304–324.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Species sampled in a boreal forest landscape in central Sweden, with notes on biological and conservation status information (Red-list or pest status).

**Appendix S2** Characteristics of sampled stands of four types.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/ j.1472-4642.2007.00350.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.