Biological Conservation 144 (2011) 2061–2067

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Systematic review

Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests

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ARTICLE INFO

Article history:
Received 15 October 2010
Received in revised form 7 February 2011
Accepted 13 February 2011
Available online 26 May 2011

Keywords:
Biodiversity
Conservation
Evidence-based
Meta-analysis
Production forests
WKH

ABSTRACT

The concept of Woodland Key Habitats (WKH, small-scaled presumed hotspots of biodiversity) has become an essential component of biodiversity conservation in Fennoscandian and Baltic forests. There have been debates over the importance of WKHs in relation to the conservation of biodiversity in production forests. We applied a systematic review protocol and meta-analysis to summarize knowledge on comparisons of biodiversity qualities, such as dead wood and species richness, between WKHs and production forests in relevant countries. We also summarized the knowledge on the impact of edge effects by comparing WKHs surrounded by production forests to WKHs surrounded by clear cuts. Studies had been conducted in Finland, Norway and Sweden. Based on our meta-analysis, WKHs seem to be relative hotspots for dead wood volume, diversity of dead wood, number of species and number of red-listed species. There were some differences also between countries in these biodiversity qualities. Only two studies compared WKHs surrounded by production forests and clear cuts, respectively. Hence, the capability of WKHs to maintain their original species composition and support species persistence over time remains to be addressed, as well as their role in relation to other conservation tools.

1. Introduction

Globally, habitat depletion and fragmentation have contributed to the current rampant loss of biodiversity. In the boreal forest zone, the total forest area is not decreasing but habitat availability has rapidly diminished due to habitat degradation as a consequence of effective logging and intensified silvicultural practices. Before industrialization the forests were utilized in a less intensive manner by burnbeating, tar and potash production, and thinning (Esseen et al., 1997). From the beginning of 20th century, forest harvesting methods in Fennoscandia shifted from selection felling towards clear cutting. Intensive forest management altered the species composition and the structure of the forests from old-growth to young, even-sized, single-aged forest stands (Östlund et al., 1997; Löfman and Kouki, 2001). Forestry also reduces natural disturbances and decreases the volume of dead wood (Esseen et al., 1997). Natural forests are primary habitats for a substantial number of threatened species and forestry is the main cause of species endangerment (Rassi et al., 2001), especially due to the reduction of dead wood (Siitonen, 2001), and large living deciduous trees (e.g. Berg et al., 1994). In Finland, 20–25% of all the forest-dwelling species are dependent on dead wood, and many of them are very specific in their substrate requirements making dead wood and dead wood diversity important biodiversity qualities (Siitonen, 2001). Although not always related to human impact, and thus claimed to have limitations as a measure of biodiversity (e.g. McGill et al., 2007), species richness is often applied as a measure of biodiversity since it gives a common currency for the comparisons of communities.

Forest conservation has traditionally concentrated on establishing large forest reserves. Such reserves are vital due to their ability to maintain many taxa and ecological processes but establishing them also has its constraints. One of the main constraints is the limited area available for conservation (Lindenmayer and Franklin, 2002); large continuous areas of intact forests simply do not exist anymore in Fennoscandia, particularly in the southern boreal zone. Many areas of high priority for nature conservation are located on unprotected, productive private lands (Knight, 1999). However, protecting privately owned land for biodiversity involves many challenges. For example, traditional obligatory approaches, such as acquisition of land by government have resulted in an intense resistance by land owners (e.g. Hansson, 2001; Wätzold and

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doi:10.1016/j.biocon.2011.02.016

Schwerdtner, 2005). To respond to these challenges, there has been a shift in North Europe from total protection of segregated areas to integration of forest management and conservation in a more integrated way (Parviainen and Frank, 2003) and the focus of conservation has shifted towards multiscale conservation measures (Lindenmayer and Franklin, 2002). In addition to large ecological reserves, conservation measures at lower scales, like setting aside small biological hotspots and green tree retention, are taken place in the matrix.

Protection of small parcels of forest with large ecological values is considered a cost-efficient way to conserve biodiversity in managed and fragmented forest landscapes (Lindenmayer and Franklin, 2002; Wikberg et al., 2009). One tool for conservation of the forest biodiversity in the matrix in north European countries is the setting aside of small habitat patches called Woodland Key Habitats (WKHs). WKHs are small habitat patches that are supposed to be particularly valuable for the biodiversity of production forests i.e. rich in biodiversity qualities (biodiversity hotspots). In Fennoscandia and Baltic countries the concept of WKH has gained particular attention among forest managers and forest owners, and extensive inventories of them have been conducted (Timonen et al., 2010). The WKH concept is based on two assumptions. First, red-listed species are presumed to be clustered into certain sites or habitats (rarity hotspots) rather than to occur evenly or randomly in the forest landscape. Second, it should be possible to identify WKHs by their structural features as well as indicator species, and thus direct observation of red-listed species should not be necessary (Nitare and Norén, 1992).

WKH definitions differ between countries and emphasize either primary habitat factors, such as soil and bedrock properties, or secondary factors, such as stand structure and occurrence of indicator species. The number of WKHs varies from about 5500 in Estonia and Lithuania to more than 100,000 in Finland (Timonen et al., 2010). The mean size of the WKHs varies considerably, from 0.7 ha (Finland) to 4.6 ha (Sweden). WKHs are legally protected in some of the countries (Finland, Estonia and Latvia), and overall they are protected on a voluntary basis or by forest certification (Timonen et al., 2010).

There have been debates over the conservation value of WKHs. Some studies have shown that WKHs indeed foster red-listed species (Gustafsson et al., 1999; Gustafsson, 2002; Perhans et al., 2007) but other studies have failed to unequivocally support the hotspot status of WKHs (Gustafsson, 2000; Johansson and Gustafsson, 2001; Gustafsson et al., 2004; Sverdrup-Thygeson, 2002; Pykälä et al., 2006). Hanski (2005) stated that WKHs have a marginal role in sustaining biodiversity due to their small size and scattered occurrence. Further, small sites might have difficulties to retain their original species composition and support species persistence over time since clear cutting, the prevailing logging method, in the surroundings may cause changes in the microclimatic conditions due to increased exposure to sunlight and wind. Moreover, species dispersal into WKHs might be higher when they are surrounded by mature forests rather than by clear cuts. Berglund and Jonsson (2005) reported that the populations of lichens and fungi were not in stochastic equilibrium in WKHs and therefore are likely to decrease in the future due to the transient dynamics. Consequently, studies on edge effects are relevant when the efficiency of WKHs is to be evaluated. The aim of our study was to undertake a systematic review of WKHs with special focus on comparisons of biodiversity qualities between these presumed hotspots and surrounding production forests, and also on the impact of edge effects on WKHs. To be a cost-efficient tool sustaining biodiversity in managed forest landscape WKHs should contain a higher number of the biodiversity qualities than the surrounding production forests of similar age, and these qualities should persist even if surrounding forests were clear cut.

2. Methods

Conducting a systematic review follows a certain set of guidelines that include protocol formation, data search strategy, data inclusion, data extraction, and analysis (Pullin and Steward, 2006). For the statistical analysis of the data we used meta-analysis which conducts summary analyses from the data extracted from the original studies. Full details of the systematic review can be viewed at http://www.environmentalevidence.org/SR81.html.

2.1. Search strategy and study inclusion criteria

Searching of studies was conducted during April and May 2009. Additional searches were conducted in November 2009. Initially, keywords for searching were tested to identify the most relevant ones, and to find out whether there were enough studies to motivate a review. These preliminary searches were made in ISI Web of Knowledge. The scoping resulted in omitting combinations with 'woodland key habitat' and the name of individual countries since we could combine all the countries into one search keyword. We also decided to add the new keyword 'deciduous tree' since some references known to us beforehand were using deciduous trees as a biodiversity quality measure (Appendix). The following search terms were used for the final search: (woodland key habitat)* AND (species richness, red-listed species, red listed species, redlisted species, dead wood, production forest*, managed forest*, clear-cut, clear-cut, clearcut, hotspot*, biodiversity, deciduous tree*). We also combined the search term "key habitat" and the search terms listed above. We also added different countries for these searches. An example: Key habitat AND species richness AND Sweden OR Finland OR Norway OR Latvia OR Lithuania OR Estonia OR Russia. In the final literature searches, the following databases were used: ISI Web of Knowledge, Web of Science®, BIOSIS Previews®, CABI: CAB Abstracts®, Food Science and Technology Abstracts ™, Journal Citation Reports® and Scopus. In these, all relevant references were examined.

Searches were also conducted in Google Scholar. For these, the first 100 hits were scrutinized and included in the review, if relevant. In addition to searches in English in this database, search strings were also translated to Swedish and Finnish, to guarantee retrieval of all relevant sources from the two countries, in which WKH surveys have been most extensive.

Main institutions in Sweden (Swedish Forest Agency) and Finland (Forestry Development Centre Tapio and Metsähallitus) with activities around WKHs were also consulted through personal contacts and web-page searches. Researchers with much experience of WKH research were also contacted to obtain possible unpublished results. The sources retrieved were assessed for inclusion in the review based on a hierarchical assessment of relevance first by looking at the title only (if the number of hits was >500), then abstract and finally reading the full text of the article. To assure that we did not miss any relevant study, when there were uncertainties, we included a study to the next step. Finally we judged a study to be relevant if it reported a comparison in biodiversity qualities between (1) WKHs and production forests, or (2) between WKHs surrounded by production forest and WKHs surrounded by clear cuts.

We accepted articles in peer-reviewed journals, book chapters, theses, or reports from governmental or non-governmental organizations, as well as other types of grey literature. The material found was categorized into three quality categories (see Appendix):

1. Peer-reviewed articles from internationally recognized journals, books, book chapters.
2. Reports, non-peer reviewed journal articles, Masters and PhD theses.
3. Unpublished grey literature.

2.2. Data extraction

Relevant studies had been performed in Finland, Norway and Sweden. There were no relevant studies found from the Baltic countries or Russia. We compiled a summary including qualitative data from the studies judged relevant (Appendix). Quantitative data were compiled for subsequent meta-analysis (author, year, biodiversity qualities, country and study area, vegetation zone, habitat size, test statistics (t, z, F, X^2 etc.), d.f. or sample size, mean values and a measure of variability). For the studies that met the selection criteria, data were extracted by the first author, and entered into a spreadsheet. To control for the possible data retrieval errors, data from a sample of the papers were re-extracted independently by the three other authors. Multiple data points were extracted from single studies in case the study reported several biodiversity qualities (e.g. volume of dead wood or red-listed species number) or if the single biodiversity quality could be derived independently for different study areas.

2.3. Data synthesis

The definitions and implementation of the WKH concept differ between Finland, Norway and Sweden (Timonen et al., 2010). Therefore, we expected that such differences may translate into ecological differences as well. Vegetation zone may also have an impact on biodiversity qualities, such as dead wood and dead-wood associated species. Hence, in addition to the comparisons of biodiversity qualities between WKHs and production forests we also analyzed differences among countries and among boreal forest zones. In order to retain enough data points for vegetation zones we categorized vegetation zones into three groups: (1) sub-boreal (nemoral and hemiboreal combined), (2) southern boreal and (3) middle-northern boreal (middle and northern boreal combined).

To test the hotspot status of WKHs we compared biodiversity qualities between WKHs and production forests of similar age (mature or older). If a study included different types of production forest (mature and young forest) we only included WKH vs. mature forests comparison because younger production forests presumably have lower biodiversity qualities. To test for WKHs ability to sustain biodiversity qualities we aimed at comparing WKHs surrounded by mature production forests (no edge effect) with WKHs surrounded by clear cut or sapling stands (strong edge effect).

2.3.1. Meta-analysis

The chief purpose of a meta-analysis is to provide an estimate of the true effect based on all studies that are available. To obtain this estimate, different test statistics, means and variances or simple significance levels are first transformed into a common currency called effect size and then combined (Rosenthal, 1991; Gurevitch and Hedges, 1993; Cooper and Hedges, 1994). In this systematic review we have conducted meta-analyses using MetaWin 2.0 (Rosenberg et al., 2000).

The structural biodiversity qualities that we extracted and analyzed from the data were the volume of dead wood, diversity of dead wood and volume of deciduous dead wood. Dead wood volume in WKHs and production forests were only compared from Finland and Sweden due to low number of studies from Norway. The inventory methods of dead wood varied between studies; some of the studies took into account only dead wood with a diameter of 5 cm or more from the breast height whereas others used the limit of 10 cm. The total volume of dead wood and deciduous dead wood in one of the studies was estimated using equations developed by Näslund (1947) and Eriksson (1973) (Djupström et al., 2008). Siitonen et al. (2009) calculated dead wood and deciduous dead wood volume by using volume equations based on tree species, diameter of breast height and height (Laasasenaho, 1982). Sippola et al. (2005) calculated the volume of CWD (coarse woody debris) by using the formula for the volume of a cylinder (CWD pieces) and for the entire dead trees the volume was taken from volume tables (Laasasenaho and Snellman, 1998). Diversity of dead wood was calculated as the number of different dead wood types at each site or sample plot (Djupström et al., 2008; Hottola and Siitonen, 2008; Siitonen et al., 2009). Within each study these parameters were calculated in the same way for WKHs and production forests.

In order to test whether WKHs are species richness hotspots we extracted the mean number of species (observed species richness) from the WKHs and production forests from each of the relevant studies. However, a few of the studies reported only the mean number of species records (number of observed individuals or fruiting bodies per species) and not the mean species number. To utilize the most of the available data we used both of these as hotpots indicators so that the mean species number was preferred and the mean species record was only used when the mean species number was not reported. The overall difference in diversity between WKHs and production forests might be dependent on the indicator that is being used i.e. mean number of species records and mean number of species. Thus, we tested whether the effect size differed between these two indicators by only using data from two studies including both indicators. The effect size was stronger (mean effect size = 0.79, 95% Bootstrap confidence interval 0.44–0.93) when summary analysis was conducted using mean number of species compared to mean number of species records (mean effect size = 0.33, 95% Bootstrap CI 0.25–0.39). We also analyzed the possible differences of effect sizes from all the data, using mean number of species and mean number of records separately. The effect size was slightly stronger when only data of mean number of species was analyzed (mean effect size 0.32, 95% Bootstrap CI 0.12 to 0.45) compared to mean number of records (mean effect size 0.23, 95% Bootstrap CI 0.07–0.46). Therefore, we concluded it to be safe to use both indicators in our analyses.

For each data point we calculated the difference between the mean value of the WKHs and the mean value of mature production forests, with a positive effect size denoting that the biodiversity quantity is more abundant in WKHs. Since the summary information is presented in different forms in different studies a common currency is needed. We first calculated student's t-value for each difference if means and their standard deviations were available. Then we transformed these parameters to a product moment correlation and calculated effect sizes from correlation coefficients (Cooper and Hedges, 1994). Fisher's z-transformations were used during the calculations as recommended (Rosenthal, 1991; Sokal and Rohlf, 1995). If standard deviations were missing we calculated the effect size using data on sample size and p-values of the primary study (see, Rosenthal, 1991, p. 19).

We fitted random-effects models with the data as implemented in MetaWin 2.0. In this way, we considered the correlation coefficient estimated for each experiment to be drawn from an underlying distribution of correlations rather than considering each experiment as providing an estimate of a single common value (Cooper and Hedges, 1994; Hedges, 1994; Raudenbush, 1994). Mean effect size can be considered significantly different from zero if its 95% confidence interval (derived by bootstrapping) does not include zero. To determine whether the effect sizes are homogenous we tested the heterogeneity (Q) against a χ^{2-} distribution with $n - 1^{\circ}$ of freedom. A significant Q denotes that the variance among effect sizes is greater than expected by sampling error (Rosenberg et al., 2000) and that different studies provide inconsistent effect sizes. Heterogeneity was examined always prior to running the meta-analysis.

The presence of publication bias was examined by analyzing a rank correlation (effect size vs. sample size). A significant correlation may indicate a publication bias where only larger effect sizes are likely to be published with small sample sizes (Rosenberg et al., 2000; Kotiaho and Tomkins, 2002; Tomkins and Kotiaho, 2004). We also calculated fail-safe numbers to estimate the magnitude of the publication bias. Fail-safe number is the number of unpublished, missing or non-significant studies that would need to be added to a meta-analysis so that the result of the meta-analysis would change from significant to non-significant (Rosenberg et al., 2000). Rosenthal (1979) suggests that the fail-safe number should be at least $5n + 10$ (where n is the original number of studies). In addition to the calculation of fail-safe number of the entire data set, we calculated fail-safe numbers also separately for each of the analyzed effect size.

3. Results

3.1. Review statistics

Total number of studies found from databases was 1443. The number of hits gained from the Google Scholar search in English was in total 8080 but all studies found here were already retrieved from the previous electronic database searches. Forty studies remained after the abstract filtering stage, from which 35 were found via the electronic database searches, two from the Google Scholar searches in Finnish, and two from the consultation with the main authors. No studies were found from the Google Scholar searches in Swedish. Most studies were conducted in Sweden and Finland, two studies in Norway, and none were found from the Baltic countries or Russia. Most of the studies (16) were directed towards comparisons between WKHs and surrounding production forests. Only two studies compared WKHs surrounded by mature forests and clear cuts, respectively and thus this aspect was not possible to analyze further in the review. Consequently, at the end, 18 relevant studies were included (Appendix).

3.2. Publication bias

We did not detect a significant publication bias ($r_S = -0.15$, $P = 0.100$, n = number of data points = 117). The Rosenthal's fail-safe number of the entire data set was 17,580. When calculated separately for each of the analyzed effect sizes the fail-safe number did not quite reach the critical value of $5n + 10$ for the dead wood diversity ($N = 49.6$ when the critical value was $5 \times 11 + 10 = 65$), and for the volume of deciduous dead wood the fail-safe number was 0.0 which obviously is not enough. The fail-safe number for the other biodiversity qualities were large enough and thus results of the meta-analysis can be treated as robust estimates of the true effect.

3.3. Meta-analysis

3.3.1. Dead wood

When comparing the dead wood volume in WKHs and production forests between-country heterogeneity was not significant ($Q = 0.95$, d.f. = 1, $P = 0.379$) suggesting that the studies from different countries provide consistent results. Likewise, the heterogeneity between vegetation zones was not significant ($Q = 1.44$, d.f. = 2, $P = 0.576$). Finally, overall heterogeneity was not significant ($Q_T = 30.74$, d.f. = 30, $P = 0.428$) indicating that all the 31 data points provided consistent information about the difference in dead wood volume between WKHs and productions forests. The mean effect size for dead wood volume was significantly different from zero (mean effect size = 0.41; 95% Bootstrap CI 0.26–0.52,

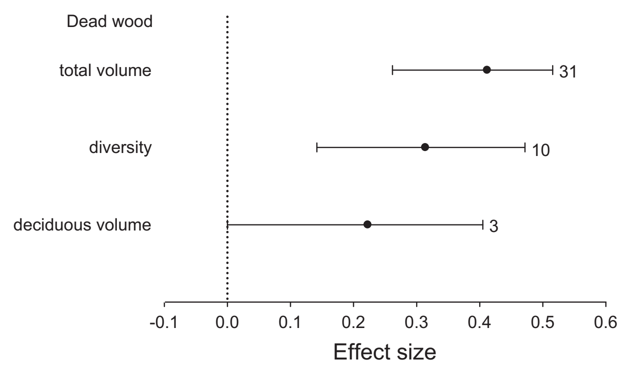

Fig. 1. Effect sizes for dead wood variables (differences in dead wood variables between WKHs and production forests). Dots represent the mean effect sizes and the error bars are equivalent to 95% Bootstrap confidence intervals. The dashed vertical line represents no difference i.e. if the confidence interval bracket zero the difference is not significant. The numbers represent sample sizes.

Fig. 1.) indicating that the volume of dead wood is significantly higher in WKHs (mean in the original data 19 $m^3\ ha^{-1}$) than in production forests (mean in the original data 11 $m^3\ ha^{-1}$).

We could not analyze the differences between WKHs and production forests in respect of the diversity of dead wood with country as a grouping variable since there was not enough data from each of the countries. We were able to analyze the data with vegetation zone as a grouping variable. However, there was not enough data from the sub-boreal vegetation zone and the comparison was conducted only between middle-northern and southern boreal zones. The heterogeneity was not significant ($Q = 0.007$, d.f. = 1, $P = 0.934$) indicating that studies from the different vegetation zones provide consistent results. The overall heterogeneity was neither significant ($Q_T = 7.73$, d.f. = 9, $P = 0.561$). The mean effect size differed significantly from zero (mean effect size = 0.33; 95% Bootstrap CI 0.19–0.46, Fig. 1) suggesting that the diversity of dead wood is significantly higher in WKHs compared to the production forests. In the original data, dead wood diversity was 1.67 times higher in the WKHs than in the production forests.

There was not enough data to analyze differences of deciduous dead wood volumes in WKHs and production forests with country or vegetation zone as a grouping variable, but the overall heterogeneity was not significant ($Q_T = 1.65$, d.f. = 2, $P = 0.438$). The mean effect size was positive (mean effect size 0.23; Bootstrap CI l 0.00–0.41, Fig. 1), indicating greater deciduous dead wood volumes in WKHs than in production forests.

3.3.2. Species richness

There was no significant heterogeneity in mean number of species between WKHs and production forests among the countries or vegetation zones ($Q = 3.82$, d.f. = 2, $P = 0.184$ and $Q = 1.61$, d.f. = 2, $P = 0.451$, respectively). Similarly, overall heterogeneity was not significant ($Q_T = 34.51$, d.f. = 34, $P = 0.443$). Mean effect size was significantly positive (0.37; 95% Bootstrap confidence interval 0.24–0.50, Fig. 2) suggesting higher overall mean number of species in WKHs than in production forests (WKHs had 1.5 times more species). We also studied whether different species groups (saproxylic beetles, bryophytes, lichens, polypores, and vascular plants) differed between WKHs and production forests. There was significant heterogeneity between the species groups ($Q = 11.62$, d.f. = 4, $P = 0.038$). All of the effect sizes were positive and most of the species groups were significantly more abundant in WKHs than in production forests (Fig. 2), most pronounced for vascular plants (1.3 times more species in WKHs than in production forests). The

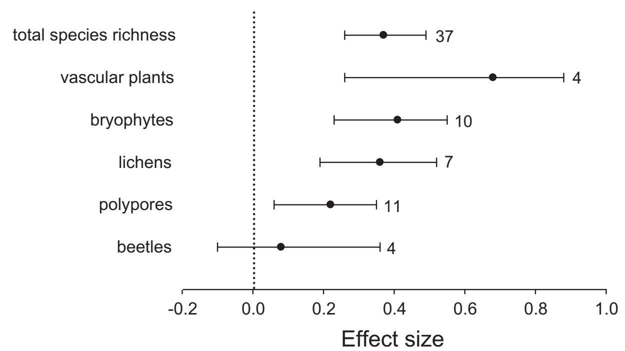

Fig. 2. Effect sizes for total species richness and separately for different taxonomic groups. For explanations, see Fig 1.

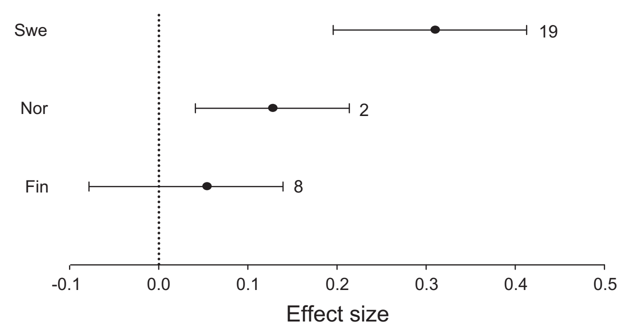

Fig. 3. Effect sizes for species richness of red-listed species in Sweden, Norway and Finland. For explanations, see Fig 1.

significant heterogeneity arises from the fact that for beetles the difference was weaker and not statistically significant (Fig. 2).

3.3.3. *Red-listed species*

For red-listed species richness between WKHs and production forests the overall heterogeneity was not significant ($Q_T = 27.13$, d.f. = 27, $P = 0.457$). There was a nearly significant heterogeneity between the countries ($Q = 8.22$, d.f. = 2, $P = 0.051$) indicating a country-specific effect sizes. In all countries, the mean effect size was positive indicating that more red-listed species were found in WKHs than in production forests, but the difference was not significant in studies from Finland (Fig. 3). In Sweden the mean effect size was the highest and more pronounced than in Norway or Finland.

We also analyzed the differences in red-listed species between WKHs and production forests with vegetation zone as a grouping variable. The heterogeneity was not significant ($Q = 4.49$, d.f. = 2, $P = 0.136$), which indicates that the difference between WKHs and production forests is not dependent on vegetation zone.

4. Discussion

In general, the lack of data is a common problem in systematic reviews (Steward et al., 2005). We only found 18 studies that fulfilled the selection criteria for our meta-analysis, from which only two studies examined species persistence in WKHs. Also, the variable methodologies used in different studies complicated the interpretation of results. Although the interpretation should be made with caution, we consider the overall result that WKHs have higher biodiversity qualities than comparable mature production forests, to be reliable and robust.

WKHs seem to be biodiversity hotspots when we consider the volume of dead wood, diversity of dead wood, bryophytes, lichens, polypores, vascular plants and red-listed species. The definitions of WKHs in all of the countries do underline the importance of structural elements (Timonen et al., 2010) and thus the result of WKHs containing more dead wood could be expected. The average volume dead wood of 19 $m^3\ ha^{-1}$ in the studied WKHs is notably more than the average volume of CWD (coarse woody debris) of production forest in general that varies between 2 and 10 $m^3\ ha^{-1}$, depending on the region (Siitonen, 2001). However, according to Siitonen (2001) the average volume of CWD in old-growth forests in southern Fennoscandia is 60–90 $m^3\ ha^{-1}$. The definition of Finnish WKHs states that these habitats should be in natural or natural-like state (Meriluoto and Soininen, 1998) but the small volume of dead wood in Finnish WKHs compared to the old-growth forests suggests that these sites are not in such a state. The result of deciduous dead wood being more abundant in WKHs is only suggestive since the effect size was only indicative and the sample size was rather low.

WKHs did host more species than mature production forests in all of the countries. Indeed, only in one Finnish study there were more species outside than inside WKHs. Sippola et al. (2005, see Appendix) found more polypore species in production forests than in WKHs. In this study, surrounding forests also contained higher volume of dead wood. The amount of dead wood correlates strongly with polypore species richness (Junninen and Komonen, 2011) and this could explain the higher polypore species number in production forest. The study was carried out in Koli national park where the surrounding forests to WKHs are former production forest. Thus, this study might not be representative of production forests in general.

The difference between WKHs and production forest was most pronounced in vascular plants and least pronounced in saproxylic beetles. For vascular plants it could be that in some studies, the WKHs were of special types with deviating conditions regarding soil, topography and climate known to promote this species group, like springs, brooks or ravines, and control forests were of more common forest types. For beetles, the low difference is somewhat surprising because one may expect dead wood dependent species such as saproxylic beetles to readily respond to the higher dead wood volumes in WKHs. It may be difficult to extensively sample beetle species and therefore the differences may not be easily detectable. For some species groups the sample sizes were low and the among-group differences in Fig. 2 should be considered hypotheses for future studies. We also caution against extrapolating the results to species groups not included in this study. For example, the only studied animal species group for which we had data was saproxylic beetles, and therefore, our results cannot be generalized for the fauna.

WKHs seem to be hotspots of red-listed species (rarity hotspots) in Sweden and in Norway. However, according to our analyses, WKHs in Finland do not differ significantly from production forests, at least regarding polypores which was the only group of red-listed species studied in this country. According to the Swedish definition red-listed species are likely to occur in WKHs (Nitare and Norén, 1992; Norén et al., 2002) and the Norwegian definition emphasizes habitat elements that are important for species. Finnish studies have been concentrating only on one sub-group of woodland key habitats, so called Forest Act habitats. In these habitats primary factors such as soil or bedrock properties (e.g. the chemical properties of the soil) are in focus and some weight has been put on secondary factors, such as successional stage and existence and attributes of dead wood (Timonen et al., 2010). This more narrow definition of WKHs in Finland compared with the other Fennoscandian countries is probably associated with the comparatively low occurrence of red-listed species in Finnish WKHs. However, the results from Finnish red-listed species were only from polypore species. The results from Norway should also be interpreted with caution due to the low sample size.

There were only two studies (Appendix) comparing WKHs surrounded by mature forest and clear cuts, respectively. Since WKHs are small-scale conservation areas in production forests it is expected that the surrounding forest will at some point be clear cut. Both studies reported a change in the species composition in the WKHs due to logging (Vuorinen, 2007; Hartikainen, 2008). Hanhimäki (2003) found that WKHs surrounded by clear cuts had lower relative humidity compared to the old-growth spruce forest controls. Also, the mean number of polypore species was lower in WKHs surrounded by clear cuts than in control forests. The edge effect causes changes in the microclimatic conditions due to increased exposure to sunlight and wind, thus changing species abundance and composition (Esseen and Renhorn, 1998; Snäll and Jonsson, 2001). Further, clear cutting might result in increased isolation of WKHs since the matrix quality is lowered, which decreases the dispersal possibility from the surroundings.

5. Conclusions

Based on the available data our results show that WKHs seem to be hotspots for dead wood, diversity of dead wood, species richness and red-listed species. However, even though WKHs now hold more of these attributes an open question is whether they are able to retain their original species composition and support species persistence over time. Indeed, landscape scale issues, such as proximity and extent of clear cuts, may be reducing WKHs contribution to the conservation of biodiversity. More information on this aspect is needed before the WKH's status as a functional conservation tool can fully be evaluated. It also remains to be further studied how disturbance in WKHs might create conditions for other types of species, and if post-disturbance phases have a conservation value at the landscape scale.

The results of our study give some guidelines for the forest conservation practices and also reveal the shortage of information needed for the evaluation of small-scaled conservation areas. The identification of small biodiversity hotspots like the WKHs studied in this paper is an important conservation action in many parts of the world. WKHs are conceptually related to High Conservation Value Forests (HCFVs) which is a key component of many certification standards of Forest Stewardship Council (FSC) (Jennings et al., 2003). Increasingly multi-scaled conservation models (Lindenmayer et al., 2006) are being applied in different countries, and essential in this is to set aside areas of different sizes for biodiversity conservation, with small scale levels like WKHs. In the regions where a strong clustering of biodiversity to certain sites due to environmental or historical reasons occurs, it could be motivated to identify key habitats, and include them as important components in reserve networks. However, the WKH concept has been developed to the regions where the forests have been intensively managed and hence highly fragmented. Therefore it is not advisable to uncritically apply the WKH approach to other forest landscapes that differ from Scandinavian or Baltic forest-use history e.g. in regions where larger compartments of intact forests remain under natural-like dynamics.

Acknowledgements

We are grateful to Mari Jönsson and Juha Siitonen for their help in providing data. We also want to thank Tero Toivanen and anonymous reviewers for their comments. The study was funded by the Academy of Finland (Proj. #115560) and the Finnish Ministry of the Environment (Ympäristöklusterin tutkimusohjelma). Peter Frost helped formulate the title.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.02.016.

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Appendix

Country, study area, study design, habitat size, plot size and hotspot status (in the original study) of studies included in the review.

Study	Country & study area	Study design	Habitat size (ha)	Plot size (ha)	Hotspot status (vote count) +/-
Djupström et al. (2008)	Sweden, middle boreal vegetation zone	Comparison between WKHs (N=20) and production forest sites (N=18)		Reserves, WKHs and old managed forest: min. 50m x 50m (0.25 ha) Retention patches: min. 25 x 25 m (0.07 ha)	Dead wood volume: ns Saproxylic beetles diversity: + Deciduous dead wood volume: ns Diversity of dead wood: ns Red-listed beetles: ns
Froster (2005)	Sweden, boreal forest zone	Comparison between WKHs (N=9) and production forest sites (N=9)		WKH: 0.25 PF: 0.5	Indicator bryophytes: + Indicator lichens: + Wood-living fungi: ns Vascular plants: ns
Gjerde (2007)	Norway	Comparison between WKHs (N=158) and production forest sites (N=180)		0.25	Red-listed species: +
Gustafsson (2000)	Sweden, hemi-boreal vegetation zone	Comparison between WKHs (N=10 in Roslagen, N=15 in Småland) and production forest sites (N=20)	WKHs in Roslagen 2.7 ha (0.6-4.7), WKHs in Småland 1.2 ha (0.5-3.3)	WKH: 0.20 PF: 25	Vascular plant species richness: ns Red-listed vascular plants: ns Indicator vascular plants: ns
Gustafsson (2002)	Sweden, hemi-boreal vegetation zone	Comparison between WKHs (N=10 in Roslagen, N=15 in Småland, N=10 in Örsundsbro) and production forest sites (N=20 in Roslagen and Småland, N=10 in Örsundsbro)	WKHs in Örsundsbro 1.8 ha (0.5-2.7), WKHs in Roslagen 2.7 ha (0.6-4.7), WKHs in Småland 1.2 ha (0.5-3.3)	0.2	Tot. records of red-listed species: + Bryophytes: ns Lichens: + Red-listed vascular plants: ns
Gustafsson et al. (2004)	Sweden, hemi-boreal vegetation zone	Comparison between WKHs (N=10 in Roslagen, N=15 in Småland) and production forest sites (N=20)	WKHs in Roslagen 2.7 ha (0.6-4.7), WKHs in Småland 1.2 ha (0.5-3.3)	0.2	Cumulative species richness: + Bryophyte species log ha $^{-1}$: ns Bryophyte species records per hectare: + Indicator bryophytes record per hectare: + Red-listed bryophytes per hectare: ns

Study	Country & study area	Study design	Habitat size (ha)	Plot size (ha)	Hotspot status (vote count) +/-
Hartikainen (2008)	Finland, southern boreal vegetation zone	Comparison between WKHs surrounded by clear cut (N=8) and WKHs surrounded by mature forest (N=8)	WKHs in clear cuts: 0.3 ha WKHs in mature forests: 0.2 ha		Vascular plants: -
Hottola and Siitonen, (2008)	Finland, in the border between southern boreal and middle boreal vegetation zones	Comparison between WKHs (N=69) and production forest sites (N=70)	WKHs: average size 0.7 ha (0.2-2.5ha) Ordinary managed stands: 1.7 ha (0.3-7.6 ha)	0.2	Polypore species number: + Red-listed polypores: ns Diversity of dead wood: +
Johansson and Gustafsson, (2001)	Sweden, hemi-boreal vegetation zone	Comparison between WKHs (N=10 in Roslagen, N=15 in Småland) and production forest sites (N=20)	WKHs in Roslagen 2.7 ha (0.6-4.7), WKHs in Småland 1.2 ha (0.5-3.3)		Red-listed lichen species number: ns Red-listed-lichens:ns Indicator lichens: ns
Jönsson and Jonsson (2007)	All Sweden	Comparison between WKHs (N=488) and production forest sites		0.0314	Dead wood volume: +
Junninen and Kouki (2006)	Finland, Southern boreal zone	Comparison between WKHs (N=72) and production forest sites (N=12)	WKHs: mean 0.5 ha (0.28-0.65) Production forest: 1.52		Number of polypore species:+
Korvenpää et al. (2002)	Finland, south- and middle boreal zone	Comparison between WKHs (N=180) and production forest sites (N=21)			Vascular plants: + Bryophytes: +
Perhans et al. (2007).	Sweden, middle boreal vegetation zone	Comparison between WKHs (N=20) and production forest sites (N=20)			Bryophytes: + Red-listed bryophytes: + Indicator bryophytes: + Lichens: ns Red-listed lichens: ns Indicator lichens: ns Deciduous dead wood volume: ns
Selonen and Kotiaho	Central-Finland	Comparison between WKHs (N=20) and production forest (N=20)	Study sites: 0.1 ha	0,1	Volume of dead wood: + Diversity of dead wood: + Deciduous trees: + Polypores: + Bryophytes: + Saproxylic beetles: ns

Study	Country & study area	Study design	Habitat size (ha)	Plot size (ha)	Hotspot status (vote count) +/-
Siitonen et al. (2009)	Finland, in the border between southern boreal and middle boreal vegetation zones	Comparison between WKHs (N=70) and production forests (N=70)	WKHs: average size 0.7 ha (0.2-2.5ha) Ordinary managed stands: 1.7 ha (0.3-7.6 ha)	0.2	Volume of dead wood: + Diversity of dead wood: + The number of large deciduous trees: +
Sippola et al. (2005)	Finland, at the transition border of the southern and middle boreal vegetation zones	Comparison between WKHs (N=15) and former production forest sites (N=5)	3 classes of WKHS: a) <0.10 ha b) 0.15-0.50 ha c) >1 ha Old-growth forest: 6-15 ha		Total volume of CWD: + Polypore species number: - Red-listed and indicator polypore species number: -
Sverdrup-Thygeson (2002)	Norway, boreal forest	Comparison between WKHs (N=30) and production forest (N=30)		PF: 0.16	Saproxylic beetles: ns Red-listed beetles: ns Indicator beetles: ns Structural characteristics: ns
Vuorinen (2007)	Finland, southern boreal vegetation zone	Comparison between WKHs surrounded by clear cut (N=8) and WKHs surrounded by mature forest (N=8)	WKHs in clear cuts: 0.3 ha WKHs in mature forests: 0.2 ha		Bryophytes: ns

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