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ARE WOODLAND KEY HABITATS BIODIVERSITY HOTSPOTS IN BOREAL FORESTS?

Systematic Review

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Summary

1. Background

The concept of Woodland Key Habitats (WKH, small-scaled presumed hotspots of biodiversity) has become an essential component of forest management in Fennoscandian and Baltic countries. There have been debates over the importance of WKHs in relation to production forests, and several research projects have focused on differences in biodiversity between the two. Results have been contradictory, and thus there is a need to summarize and clarify the existing knowledge.

1. Objectives

Our objective was to summarize knowledge on comparisons of several biodiversity qualities between WKHs and production forests in relevant countries i.e. the countries where WKH concept has been implemented. We also summarize the knowledge on the impact of edge effects on WKHs by comparing WKHs surrounded by mature forests to WKHs surrounded by clear cuts.

2. Methods

We conducted searches in multiple databases and in Google Scholar after the keyword scoping. Main institutions in Sweden (Swedish Forest Agency) and Finland (Forestry Development Centre Tapio and Metsähallitus) with activities on 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 Researchers with much experience of WKH research were also contacted to obtain possible unpublished literature. We conducted meta-analysis with the data extracted from the original studies that were included it the review.

3. Main results

Studies had been conducted in Finland, Norway and Sweden. Total number of studies found from databases was 1443. Forty studies remained after the abstract filter stages. Finally, 18 studies were included in the review, from which 16 studied the differences between WKHs and production forests, and only two studies compared WKHs surrounded by mature forests and WKHs surrounded by clear cuts. Our results suggest that WKHs seem to be hotspots of dead wood, diversity of dead wood, species richness and red-listed species. Also, we found differences between countries in these biodiversity qualities.

4. Conclusions

Our results suggest that WKHs seem to be biodiversity hotspots. However, there are not enough studies focusing on how WKHs are able to maintain these biodiversity qualities when surrounded by clear cuts. Indeed, landscape scale issues, such as proximity and extent of clear cuts, may be reducing WKHs contribution to the conservation of biodiversity. As such this area needs further investigation.

Main Text

1. Background

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 intensive logging and 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 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 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 (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 to sustain 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. Objectives

2.1 Primary objective

To systemically collate and synthesize published and unpublished evidence originating from the Fennoscandian and Baltic countries as well as Russia, in order to address the following questions:

1. "Are Woodland Key Habitats (WKH) biodiversity hotspots (i.e. do they have higher biodiversity qualities) compared to production forests?"
2. "Is there a difference in biodiversity qualities between WKHs surrounded by production forest and WKHs surrounded by clear cuts?"

Listed below are the biodiversity qualities that were being studied to assess the hotspot status in primary question 1., and to compare the differences between WKHs in primary question 2. There were no limitations to taxa and the geographical scope was in Fennoscandian and Baltic countries, and in Russia.

1. red-listed species richness
2. total species richness
3. volume of dead wood
4. dead wood diversity
5. volume of dead deciduous trees
6. volume of deciduous trees

3. Methods

3.1 Question formulation

The question composed two elements:
1. *Subject* : WKHs surrounded by the production forest and WKHs surrounded by clear cuts
2. *Outcome*: WKHs are or are not hotspots for biodiversity, WKHs surrounded by production forest are richer or poorer in biodiversity qualities compared to WKHs surrounded by clear cuts or there are no differences

3.2 Search strategy

In order to collate information for the review the following steps were carried out:

3.2.1 Review scoping
The keywords were tested firstly to find the most relevant ones, and secondly, to determine whether there are enough studies conducted to warrant a review. This was done by using the following keywords in ISI Web of Knowledge search:

Keyword 1		Keyword 2	Hits
Woodland key habitat*			291
Woodland key habitat*	AND	species richness	54
	AND	red-listed species	30
	AND	dead wood	33
	AND	production forest*	28
	AND	managed forest*	30
	AND	clear cut*	7
	AND	hotspot*	4
	AND	biodiversity	93
	AND	Sweden OR Finland OR Norway OR Latvia OR Lithuania OR Estonia OR Russia ***	>100 000
	AND	deciduous tree*	¤
Key habitat*	AND	species richness	573
	AND	red-listed species	40
	AND	dead wood	111
	AND	production forest*	225
	AND	managed forest*	126
	AND	clear cut*	38
	AND	hotspot*	61
	AND	biodiversity	1,116
	AND	Sweden OR Finland OR Norway OR Latvia OR Lithuania OR Estonia OR Russia	>100 000
	AND	deciduous tree*	¤

After the scoping the list of keywords remained mostly the same. However, we decided to not combine keywords “Woodland key habitat” and countries (marked by ***). We also decided to add a new keyword (added and marked with ¤ in the “hit” column at the table above). With the “Key habitat”-keyword we combined one other keyword at a time plus the countries, for example: Key habitat AND species richness AND Sweden OR Finland OR Norway OR Latvia OR Lithuania OR Estonia OR Russia

3.2.2 Database search

The following databases were used for the searches (Appendix 1):

- ISI Web of Knowledge
    1. Web of Science®
    2. BIOSIS Previews®
    3. CABI: CAB Abstracts®
    4. Food Science and Technology Abstracts ™
    5. Journal Citation Reports®
- Scopus

The search terms used were:

Woodland key habitat*		
Woodland key habitat*	AND	species richness
	AND	red-listed species
	AND	dead wood
	AND	production forest*
	AND	managed forest*
	AND	clear cut*
	AND	clearcut*
	AND	clear-cut
	AND	hotspot*
	AND	biodiversity
	AND	deciduous tree*
	AND	red listed species
	AND	redlisted species

Key habitat*	AND	species richness	AND	Sweden OR Finland OR Norway OR Latvia OR Lithuania OR Estonia OR Russia OR Denmark
	AND	red-listed species	AND	
	AND	dead wood	AND	
	AND	production forest*	AND	
	AND	managed forest*	AND	
	AND	clear cut*	AND	
	AND	clearcut*	AND	
	AND	clear-cut	AND	
	AND	hotspot*	AND	
	AND	biodiversity	AND	
	AND	deciduous tree*	AND	
	AND	red listed species		
	AND	redlisted species		

3.2.3 Internet search

The first 100 results of each of the searches were considered and included in the review if relevant. The search was conducted by Google Scholar. The same keywords were used as in the database search. To make sure all relevant studies would be included to the review we also conducted similar searches in Finnish and Swedish Google Scholar. To find the studies written in Finnish or Swedish we used the Finnish or Swedish key words (equivalent to English ones) in Finnish or Swedish Google Scholar respectively. The Finnish key words were: avainbiotooppi*, elintärkeät elinympäristöt AND avohakkuu*, AND hotspot*, AND lahopuu*, AND lehtipuu*, AND monimuotoisuuden keskittymä*, AND monimuotoisuus, AND talousmetsä*, AND uhanalaiset lajit. The Swedish keywords were: Nyckelbiotop* AND artantal, AND rödlistad*, AND död ved, AND produktionsskog*, AND skött skog, AND, hygge*, AND hotspot, AND biologisk mångfald, AND biodiversitet, AND lövträd.

3.2.4 Specialist searches

The following institutions were consulted. Here we decided to restrain the organizations to Sweden and Finland due to the fact that the material from other countries would have been difficult to extract when written in native languages.

- Swedish Forest Agency (Sweden)
- Forestry Development Centre Tapio and Metsähallitus (Finland)

We also contacted personally the main authors involved in WKH research as a part of the search of unpublished grey literature.

3.3 Study inclusion criteria

The studies were assessed for inclusion in the review based on a hierarchical assessment of relevance first by looking only the title (if the number of hits in >500). If the title was relevant the abstracts were read, followed by reading the full text of articles with relevant abstracts. Abstracts were considered relevant if they fulfilled the relevancy requirements stated below. To assure that we did not miss any relevant study, when there were uncertainties, we included the study to the next step.

3.3.1 Relevant subject:

All the studies that investigate WKHs surrounded by production forests, and WKHs surrounded by clear cuts, and include collected data.

3.3.2. Types of outcome:

WKHs are or are not hotspots for biodiversity qualities, WKHs surrounded by production forest are richer or poorer in biodiversity qualities compared to WKHs surrounded by clear cuts or there are no differences.

3.3.4. Types of studies:

The selected studies were those that presented comparisons of biodiversity qualities between WKHs and production forests, and studies comparing biodiversity qualities between WKHs surrounded by production forests and WKHs surrounded by clear cuts. We accepted articles in peer-reviewed journals, book chapters, theses, or reports from governmental or non-governmental organizations. Other type of grey literature could also be included. Both quantitative and qualitative studies were included.

3.4 Data extraction

To extract information from selected studies, we compiled quantitative and qualitative data from each of the studies. The following information was extracted:

- Author
- Year
- Studied biodiversity qualities
- Country and study area
- Experimental design (what has been compared)
- Habitat type
- Habitat size

- Main result: test statistics (t, z, F, X^2 etc.), d.f. or sample size, mean values, and a measure of variability across all plots within a study.

3.5 Data synthesis

In our previous study (Timonen et al., 2010) we concluded that there are differences among the countries (Estonia, Finland, Latvia, Lithuania, Norway and Sweden) in the definitions and implementation of the WKH concept. 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).

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 Meta-Win 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 for 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). Selonen et al. (in prep.) however, used diversity index, and thus the dead wood diversity result from their study could not be included in the analysis. However, 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) 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.

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 consider 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). Each study was weighted by the reciprocal of its sampling variance (Rosenberg et al., 2000). 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 $n - 1$ degrees 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.

4. Results

4.1 Review statistics

Searching was conducted during April and May 2009. Additional searches were conducted in November 2009. The main results from the search are shown in Table 1. Forty studies remained after abstract filter stage from which 35 were found via database searches. In addition, the number of hits gained from the Google Scholar search was in total 8080. However, the relevant studies found from Google Scholar search did not contribute to the final number of relevant studies since all of the studies were already found previously from database searches. We found two relevant abstracts from The Finnish Google Scholar search and we did not find any relevant studies from the Swedish Google Scholar search. The consultation of the main authors increased the number of relevant studies by two and the consultation of institutions increased the number of relevant studies by two.

Most of the relevant studies included to this review were comparing WKHs to production forests. We only found two relevant studies comparing WKHs surrounded by production forests and WKHs surrounded by clear cuts. Therefore we were only able to find answers to the question number 1: “Are Woodland Key Habitats (WKH) biodiversity hotspots (i.e. do they have higher biodiversity qualities) compared to production forests?” The designs of all included studies were similar i.e. multiple WKHs were compared with multiple production forest sites (see Appendix).
Most of the studies were conducted in Sweden and Finland, and there were two studies conducted in Norway. We did not find any relevant studies conducted in Baltic countries or in Russia.

Table 1. Number of studies included during each of the systematic review filtering stages.

Systematic review stage	No. studies
Studies captured using search terms in electronic databases* (including duplicates)	1443
Studies captured using search terms in electronic databases* (excluding duplicates)	404
Studies remaining after abstract filter	40
Studies remaining after full text filter i.e. relevant studies (from databases, Google Scholar, and consultations)	18

*(excludes hits from Google Scholar search)

4.2 Meta-analysis

4.2.1 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 studies 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 to 0.52, figure 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 not 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 to 0.46, figure 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 to 0.41, figure 1), indicating greater deciduous dead wood volumes in WKHs than in production forests.

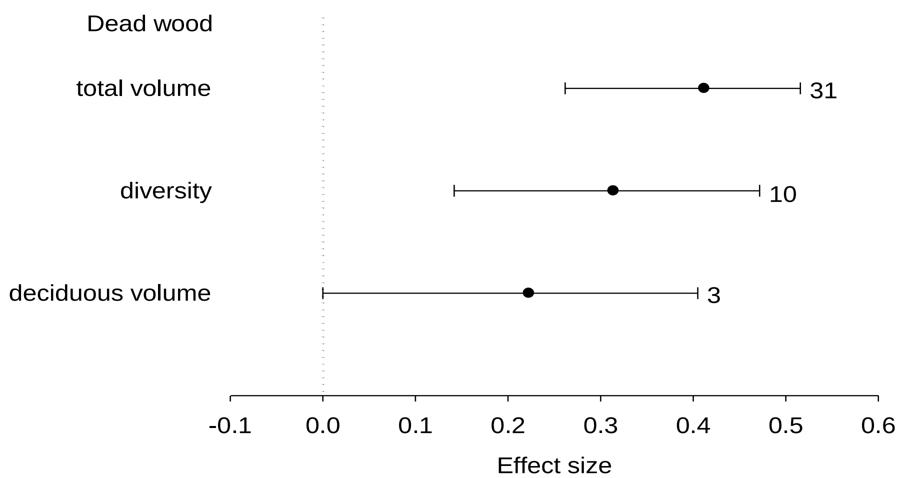

Figure 1. Effect sizes (product moment correlation) for dead wood variables (differences in dead wood variables between WKHs and production forests). Dots represent the mean effect sizes and the error bars are equivalent to 95% Bootstrap confidence intervals of the effect size across all studies. The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

4.2.2 Species richness

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 records and mean number of species (see Data synthesis). 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 to 0.93) when summary analysis was conducted using mean number of species compared to mean species record (mean effect size = 0.33, 95% Bootstrap CI 0.25 to 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 to 0.46). Therefore, we concluded it to be safe to use both indicators in our analyses.
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 to 0.50, figure 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 (Figure 2), most pronounced for vascular plants (1.3 times more species in WKHs than in production forests). The significant heterogeneity arises from the fact that for beetles the difference was weaker and not statistically significant (Figure 2).

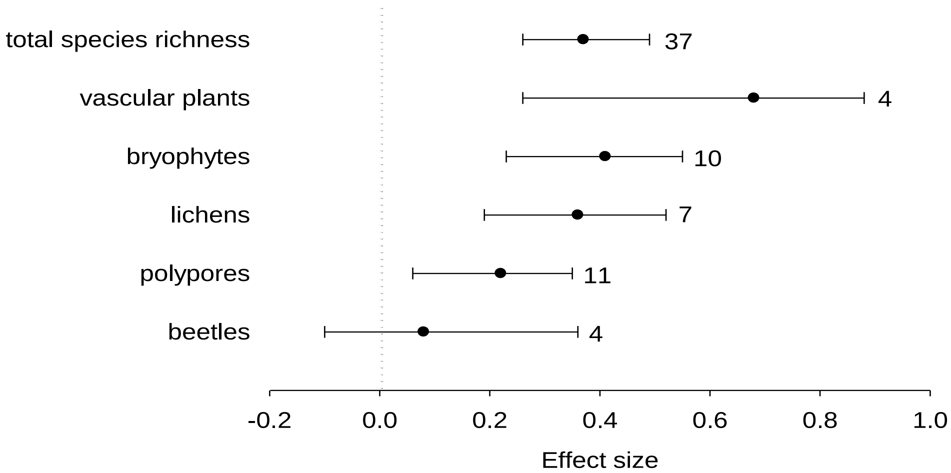

Figure 2. Effect sizes for total species richness and separately for different taxonomic groups. For explanations, see Fig 1.

4.2.3 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 (Figure 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.

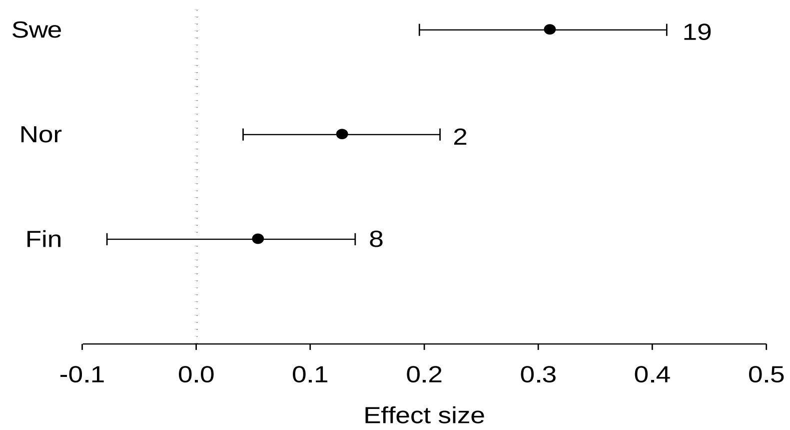

Figure 3. Effect sizes for species richness of red-listed species in Sweden, Norway and Finland. For explanations, see Fig 1.

4.3 Outcome of the review

Our results show that WKHs seem to be hotspots of dead wood, diversity of dead wood, species richness and red-listed species. However, even though they now hold more of these attributes an open question that remains to be addressed is whether WKH's are able to retain their original species composition and support species persistence over time. There are not enough studies focusing on how WKHs are able to maintain biodiversity qualities when surrounded by clear cuts.

5. Discussion

5.1 Evidence of effectiveness

Based on the studies included into this review WKHs seem to be biodiversity hotspots of dead wood and species. All the biodiversity qualities that were used in comparisons were more abundant in WKHs than in production forests. The difference between WKHs and production forests varied with different species groups i.e. some species were more abundant in WKHs that others compared to the production forests.

5.2 Reasons for variation in effectiveness

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 polypore species in production forests than in WKHs (Sippola et al., 2005, see Appendix). The study was carried out in Koli national park where the surrounding forests to WKHs are former production forest. In this study, surrounding forests also contained higher volume of dead wood. 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. This is a somewhat surprising because one may expect dead-wood dependent species such as saproxylic beetles to readily respond to a lower dead wood volumes in production forests than 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 Figure 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, in Finland WKHs did not differ significantly from production forests. These results are in line with the definition of WKHs in different countries. 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 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 Nordic 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 however be interpreted with caution due to the low sample size.

5.3 Review limitations

The status of WKH as a biodiversity hotspot is species and biodiversity quality dependent and thus the results cannot be generalized into different species groups or biodiversity qualities. For example the only studied animal species group was beetles and therefore there is lack of knowledge on animal species richness in WKHs.

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). Ylisirniö et al. (in prep.) 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.

6. Reviewers' Conclusions

6.1 Implications for conservation

WKHs seem to represent hotspots of biodiversity in production forests. Hence, the WKH concept could potentially be a relevant conservation tool when implemented well in the matrix. Multi-scaled conservation models (Lindenmayer et al. 2006) are increasingly 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. 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.

6.2 Implications for research

Research has concentrated on the current differences between WKHs and production forests. Nevertheless, in order to evaluate the WKH concept as a valid conservation tool we need to know whether WKHs are able to maintain their species composition in a long run under the prevailing forestry procedures i.e. when WKHs are occasionally surrounded by clear cuts. Indeed, landscape scale issues, such as proximity and extent of clear cuts, may be reducing WKHs contribution to the conservation of biodiversity. As such this area needs further investigation.

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10. Appendix

Country, study area, study design, habitat size, plot size and hotspot status in the original study.

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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