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Woodland key habitats evaluated as part of a functional reserve network

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ABSTRACT

Woodland key habitats (WKHs) represent a potentially cost-efficient means to protect biodiversity in managed forests. The Forest Act of Finland defines 13 habitat types of WKHs, which enjoy legal protection. It has been argued that WKHs are too small-sized and scattered in occurrence to be actually important in the maintenance of forest biodiversity. However, from the species' perspective, WKHs form a network together with nature reserves. We evaluated the value and role of WKHs as a part of the whole reserve network using a graph-theoretical connectivity approach in three areas (ca. 500 km² each) located in Central Finland. The networks were formed separately for different habitat types and dispersal distances (ranging from 200 m to 25 km). We compared networks with and without WKHs, and thereby quantified the contribution of WKHs to overall network connectivity. We also examined the role of WKHs in the networks based on patch importance and network centrality measures. The results showed that the connectivity contributions of WKHs are tightly linked with the dispersal abilities of threatened species: WKHs enhance habitat connectivity, especially for species with an intermediate dispersal ability. For species with a poor dispersal ability, the protection of large set-asides would be a more efficient way to increase habitat connectivity than WKHs. WKH-based conservation seems to improve the connectivity of naturally rare and scattered habitat types relatively more than common habitat types, but in sparse networks a greater dispersal ability is required to gain enhanced connectivity than in dense ones. The connectivity value of WKHs can be understood as an emergent and scale-dependent property, appearing at the level of the entire functional network. Provided that the site characteristics of WKHs can be safeguarded, they can be a valuable and efficient addition to the reserve network.

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1. Introduction

Habitat loss and fragmentation are major global threats to biodiversity, and efficient tools are needed to combat their negative effects. Supplementing existing protected-area networks is one of these tools. The history of protected-area establishment in many global regions has produced a network that is biased toward infertile landscapes that are not economically valuable for production (Pressey, 1994; Balmford and Whitten, 2003). As a consequence of bias towards landscapes of low productivity, areas of high priority for nature conservation tend to be located on unprotected private lands (Knight, 1999). Protecting privately-owned land for biodiversity involves many challenges, including the acceptance of additional conservation efforts by the landowners.

Fragmentation can intensify the effects of pure habitat loss producing potential population decline greater than expected solely on the basis of remaining area (Andrén, 1994; Bender et al., 1998) because of the loss of landscape connectivity. Connectivity has been linked to various ecological processes: it affects species

colonisation and dispersal success (van Langevelde, 2000; Moilanen and Nieminen, 2002; Walters, 2007), extinction risk (Franken and Hik, 2004), population density (Fahrig and Paloheimo, 1988; Hanski et al., 1994) and population growth rate (Fahrig and Merriam, 1985). Connectivity can thus be considered to be a desirable quality of protected-area networks. Connectivity can only be understood in the light of two components. Structural connectivity refers to the degree to which some landscape elements are contiguous or physically linked to one another (With et al., 1997; Tischendorf and Fahrig, 2000), whereas functional connectivity recognises the behavioural responses of organisms to the physical structure of the landscape (Taylor et al., 1993; Bélisle, 2005). Thus, landscape connectivity depends not only on the amount and patterning of habitat, but also on the habitat affinities and dispersal abilities of species.

Modern forestry has severely altered the overall dynamics and structure of Fennoscandian forest ecosystems, although the total area of forest land has not changed (Östlund et al., 1997). Production forests are younger, more even-aged, more homogeneous, have less dead wood and deciduous trees than natural forests (Esseen et al., 1997). As a result of intensive forest management, many forest-dwelling species have become threatened. According to the

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latest assessment, 38% of the red-listed species in Finland are forest species, and about 8% of all assessed forest species are threatened (Rassi et al., 2001). A large number of forest species has adapted to living under conditions that are not met in intensively managed forests.

Also in Fennoscandia, the majority of protected areas are located at high elevations and high latitudes, or in remote landscapes with low economic value (Nilsson and Gotmark, 1992; Virkkala, 1996; Stokland, 1997). Protected-area networks in more productive regions of Fennoscandia appear to be inadequate, and there is an imminent need to supplement the networks, particularly for forests (Angelstam and Andersson, 2001). In reaction to the notion that protected areas are not sufficient for forest biodiversity conservation, new forestry practices have been implemented in the managed forests of Fennoscandia. Woodland key habitats (WKHs) represent a new means in ecologically more sustainable forestry. WKHs are defined as habitats in which red-listed species are likely to occur (but not necessarily observed), and they are considered as sites harboring forest biodiversity (Hansson, 2001). WKHs are situated in managed forests, but still have many characteristics of natural stands. The idea in supplementing the network with WKHs is that although WKHs are usually rather small in size, they are putative biodiversity hotspots. Thus, they may represent a cost-efficient tool in safeguarding the forest biodiversity.

The Forest Act of Finland (1996/1093) defines a total of 13 distinct habitat types. The Forest Act obliges the forest owners to maintain the special features of these “habitats of particular significance”, and allows only selective felling to be practiced on the sites. Alongside with traditional reserves, WKH-based conservation, as implemented in Finland, ensures the permanent protection of WKH sites. If not designated as WKH, the sites would be managed as typical commercial forests (thinned and clear-cut according to the prevailing recommendations). In the year 2007, delimited WKH sites covered ca. 85,000 ha (0.6% of the total forest land) of the private forests in Finland (Anonymous, 2008). In this study, the term WKH refers to the WKHs enjoying legal protection, although the concept of woodland key habitats in broad terms covers also other forest habitats besides the “Forest Act habitats”. The other valuable habitats are preserved voluntarily by good forestry practices (Meriluoto and Soininen, 1998).

WKH-based conservation has received a lot of criticism, largely directed towards the small size of the WKHs and the associated aversive ecological consequences (e.g. Hansson, 2001) (covered in more detail in Section 4). The area of a delimited WKH is on average 0.62 ha (median 0.36 ha) (Yrjönen, 2004). It has also been argued that the WKHs form such a sparse network in a forest landscape that they cannot be important in biodiversity protection in the long term (e.g. Hanski, 2006; Pykälä, 2007). The too-small-too-isolated critique neglects the fact that WKHs are embedded in the landscapes together with the protected-area network. Protected areas and WKHs may have different functions in species conservation, and they should be viewed as conservation means that complement each other. Thus, the net effect of WKHs on biodiversity hinges on their ability to support the network, and the contribution of WKHs to biodiversity can only be assessed if evaluated as integrated components in the landscapes. In the past decade, a lot of effort has been put to compare WKHs and more traditional protected areas (larger set-asides). We think it is time to evaluate the combined effects and efficiency of both of the set-aside types.

Graphs are abstractions of landscapes, where patches are represented by nodes connected by links. Links stands for functional inter-patch connections, and in the landscape-ecological context they usually represent the dispersal potential or the number of dispersing individuals between patches. Graph theory and its terminology in the field of landscape ecology have been reviewed by Bunn et al. (2000), Urban and Keitt (2001), as well as Urban and

others (2009). A graph-theoretic approach makes it possible to analyse how patches are linked at various distance thresholds (i.e. dispersal abilities), which makes it possible to address the connectivity of the landscape from the species' perspective.

In this study we investigated the role of WKHs as an integral part of the traditional reserve network. We used a graph-theoretic approach to evaluate how and to what degree the WKHs support the reserve network by not only augmenting the protected habitat area, but most importantly, by creating functional connections among reserves. We tracked the amount of habitat that is functionally connected from the species' perspective to allow for spatially dependent ecological processes. We have used a habitat-based approach and not tried to account for any specific ecological processes (other than the dispersal potential among reserve patches). We think that this landscape-ecological approach may provide an insight into the value of WKHs not previously considered. We like to emphasise, however, that this is not a sufficient evaluation of the real ecological value of WKHs, as this is a product of many factors besides habitat connectivity (e.g. the habitat quality in WKHs, the effects of the surrounding matrix) (discussed later).

We wanted to shed light on the following questions: (1) How much do WKHs contribute to the connectivity of the network? (2) Are WKHs an efficient way to supplement the reserve network? Here we consider WKH-based conservation to be efficient if WKHs contribute to network connectivity more than expected by their contribution to habitat area. (3) What is the role of individual WKH patches in the network? The contribution of WKHs in the protection of rare and red-listed species obviously varies among species according to their habitat affinities and dispersal abilities. Thus we address question (4) What kinds of species benefit the most from the WKHs (in terms of habitat specialisation and dispersal ability)? We analysed the resulting network separately for different habitat types. In addition, to encompass a wide spectrum of species dispersal abilities, the networks were scrutinised using several threshold distances among patches varying between 200 m and 25 km.

It is expected that the value of WKHs may depend on the level of habitat availability in the landscape. For that reason, we compared the contribution and the role of WKHs in three areas which differed in terms of their reserve coverage and density of WKHs.

2. Materials and methods

2.1. Study area

This study was conducted in Central Finland, which extends some 240 km in the south–north direction (Fig. 1), and where forest characteristics vary in different parts of the region. In the region, forested land (including productive forest land, scrubland and barren land) covers 85.5% of the total land area, and 96.6% of this forest land is used for forestry (Korhonen et al., 2007). Pine-dominated (*Pinus sylvestris* L.) forests cover 59%, spruce-dominated (*Picea abies* (L.) Karst.) 31% and deciduous-dominated (mainly birch, *Betula pendula* Roth and *B. pubescens* Ehrh.) 9% of the productive forest land.

Due to the strict privacy protection policy of forest owners in Finland, there is no general access even for researchers to the data containing the exact locations and delimitations of WKHs. For this reason, we were obliged to restrict our analysis to three separate study areas (Fig. 1) for which data were obtainable by special negotiations. Our study areas are not a random sample of the region, but represent the overall variation in landscape structures and WKH densities across the region. Each study area covers approximately 500 km² (Table 1).

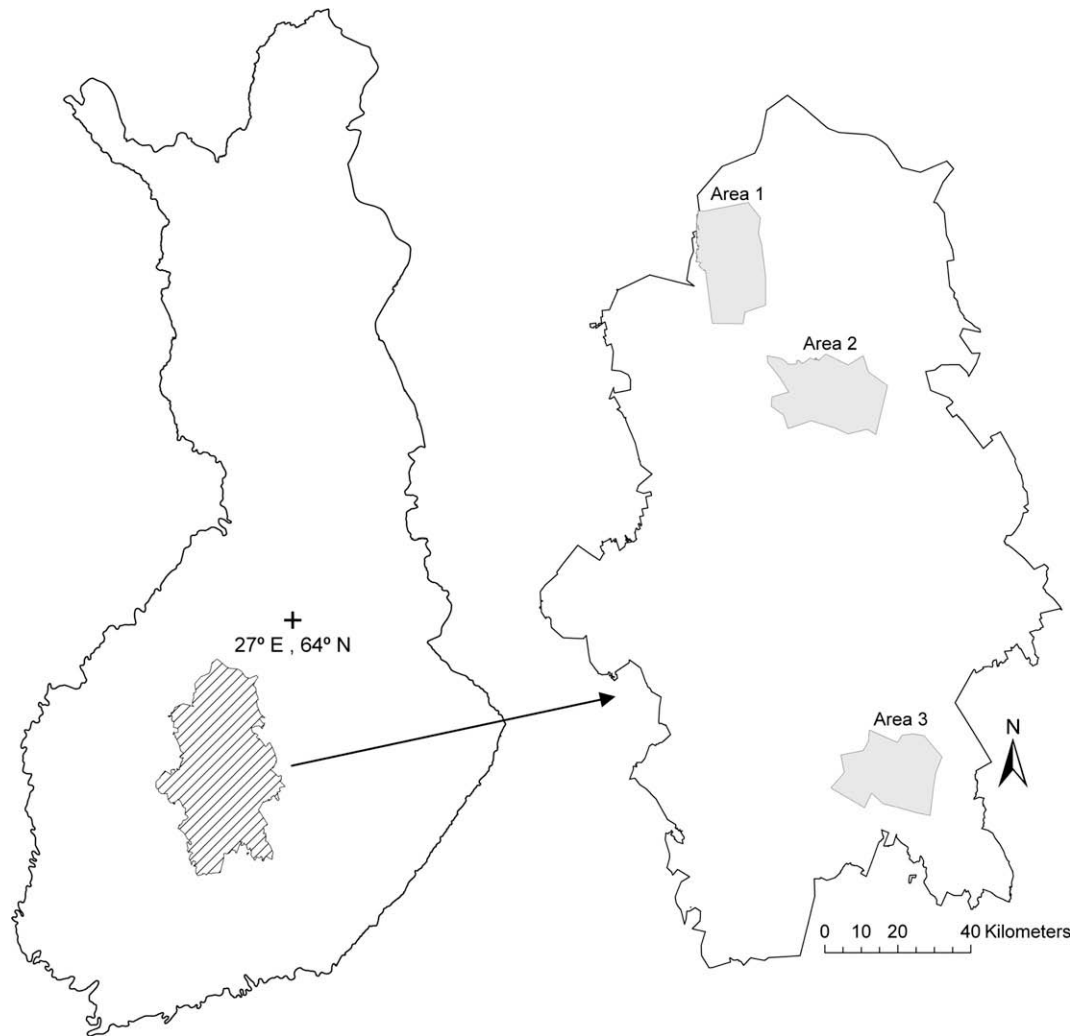


Fig. 1. The three study areas located in Central Finland.

Table 1

Areal information for the three study areas.

Measure	Area 1	Area 2	Area 3
Total area (km ²)	507	517	465
Total land area (km ²)	454	487	374
Area of forests, scrubland and barren land (km ²)	431	483	347
Total area of reserves (ha)	5749	2244	4030
Coverage of reserves (%) ^a	13.3	4.6	11.6
Number of WKHs	195	279	533
Total area of WKHs (ha)	165	215	310
Coverage of WKHs (%) ^a	0.38	0.45	0.89

^a % of area of forests, scrubland and barren land.

Area 1 is located in the middle boreal vegetation zone and represents the low-productive watershed divide area of Suomenselkä, characterised by sparsely forested mires, xeric heath forests and rocky areas. In Area 1, forests cover 65.0%, mires and bogs 9.7% and other scrublands and barren land 18.3% of the total land area (based on the national CORINE database of Finland, spatial resolution 25 m).

Area 2 is situated in the transitional zone between the southern and middle boreal vegetation zones. This region is characterised by numerous lakes and small water bodies. Forests cover 76.2%, mires and bogs 4.9% and other scrublands and barren land 15.7% of the total land area.

Area 3 is located in the southern boreal vegetation zone. This southern area of Central Finland hosts many herb-rich forests and other fertile habitat types. The vegetation in this area is more varied than in other parts of the region (Uusitalo and Paakkolanvара, 2007). Varied rock areas are also typical of this area. In Area 3 forests cover 64.6%, mires and bogs 4.5% and other scrublands and barren land 21.2% of the total land area.

The proportion of strictly protected areas (of the total area of forests and scrublands) in the whole of Finland is 8.9% (Southern Finland 2.2%; Northern Finland 15.6%). The share of strictly protected areas in Central Finland is 1.9%. When protected areas where cautious felling is allowed (WKHs, habitat types protected under the Nature Conservation Act and areas set aside by industry) are considered, the share of protected areas rises to 9.5% in the whole of Finland (Southern Finland 2.7%; Northern Finland 16.3%; Central Finland 2.5%). In our study areas, protected areas are more common than in Central Finland in general (Table 1) because all study areas host a national park, which increases their reserve coverage above the average. In Central Finland, WKHs on private lands cover 0.4% of the forestry land (compared to 0.6% in the whole country, 0.4% in Southern Finland and 0.8% in Northern Finland) (Anonymous, 2008). Coverages of WKHs in our study Areas 1 and 2 are on the average level, but Area 3 comprises more WKHs than average forest landscapes.

2.2. Landscape and habitat data

Data on the habitat types and exact locations of WKHs in the study areas were obtained from Metsähallitus (state-owned land), forest companies in the region, and from the Forest Centre in Central Finland (privately-owned forests). Fourteen landowners denied permission to data on their forest holdings, which excluded 68 WKH sites from our analyses. The excluded sites comprise 6.2% of the total number of WKHs in our three study areas, and all WKH-habitat types were represented in them. Because of this, our analyses will be conservative and the overall contribution of WKHs to the network connectivity for all habitat types is in reality somewhat greater than our results indicate.

The protected-area network included national parks, nature conservation program reserves, privately-owned protected areas, Natura 2000 areas, habitat types protected under the Nature Conservation Act, protected areas included in the regional plan, and sites protected by forest companies' own decisions. Hereafter we shall refer to all these other protected areas besides WKHs as 'reserves'. The habitat type information for the reserves was obtained from the GIS-based database administered by Metsähallitus, which contains detailed habitat type classifications for all patches in reserves. For some privately-owned reserves, habitat type information was obtained from the Regional Environment Centre and from the Regional Council of Central Finland.

Habitat type information was classified to form six habitat networks (Tables 2 and 3). All adjoining patches of the same habitat type were aggregated to present the network from the species' point of view. The reserves and WKHs were dealt with separately in the analyses, however. The networks formed a hierarchical organisation. Forest and peatlands were highest in the hierarchy, and the networks in the lower levels were subclasses of the more general networks. Networks also overlapped with each other. For example, forests and peatlands shared spruce-birch fens that foster species that are common to both habitat types. Herb-rich spruce mires were also included in herb-rich forest network as they host

species typical of herb-rich forests in addition to their own characteristic species.

A WKH can comprise more than one habitat type. For example, the immediate surroundings of brooks can also have characteristics of herb-rich forests and herb-rich spruce mires. Usually the habitat subtypes are also registered in the database, and we treated a WKH as representative of all the habitat types recorded.

2.3. Network analyses

We calculated the overall network connectivity for all six habitat networks with a threshold distance ranging from 200 m to 25 km. The increment of threshold distance was calculated as $x_{h+1} = x_h \cdot e^{0.4}$, starting with the minimum distance threshold of 200 m. This yielded a (rounded) series of distance thresholds: 200 m, 300 m, 400 m, 700 m, 1 km, 1.5 km, 2 km, 3 km, 5 km, 7 km, 10 km, 15 km and 25 km. We wanted to make the increments larger with increasing threshold distance. For poor dispersers, an increment of 100 m may have a great influence on functional connectivity, but for good dispersers only increments of kilometres in distance will matter.

For every habitat type two networks were constructed: one without WKHs and the other with WKHs. By comparing the two networks, we inferred the contribution of WKHs to the network connectivity at different threshold distances. We calculated the %-increase in connectivity that was produced by the addition of WKHs to the network. We also calculated the proportion of the overall network connectivity that was contributed by the WKHs.

Networks were analysed as undirected graphs. Link weights were determined based on Euclidean edge-to-edge distances between patches. The network interpretations were based on the Integral Index of Connectivity (IIC) (Pascual-Hortal and Saura, 2006, 2008), which ranges from 0 to 1 and is computed as:

$$IIC = \frac{\sum_{i=1}^n \sum_{j=1}^n \frac{a_i \cdot a_j}{1 + l_{ij}}}{A_L^2}$$

Table 2
Habitat networks analysed in our study. Habitat network refers to our reclassification of habitat types in reserves and WKH types outside reserves to provide six networks. The networks are to some extent hierarchical as, for example, "Forests" include habitat types and WKHs of "Heath forests".

Habitat network	Habitat types in reserves	WKH types
Peatlands	Pine mires, fens, eutrophic fens and spruce-birch fens	<ul style="list-style-type: none"> • Sparsely forested mires • Eutrophic fens • The immediate surroundings of small ponds (if not defined as flooded meadow)
Forests	Heath forests, herb-rich forests, spruce mires, wooded swamps and forests on rocky terrain	<ul style="list-style-type: none"> • Immediate surroundings of brooks, rivulets and springs (in forest area) • Fertile patches of herb-rich forests • Herb-rich spruce mires • Heathland forest islets in undrained peatland • Steep bluffs and the underlying forest stands • Gorges and ravines • Sandy soils, exposed bedrocks and boulder fields
Heath forests	Heath forests (barren, xeric, sub-xeric, mesic, herb-rich), herb-rich forests and spruce mires (excluding spruce-birch fens)	<ul style="list-style-type: none"> • Immediate surroundings of brooks and rivulets • Fertile patches of herb-rich forests • Herb-rich spruce mires • Heathland forest islets in undrained peatlands • Steep bluffs and the underlying forest stands
Herb-rich forests	Herb-rich forests, herb-rich heath forests and herb-rich spruce mires	<ul style="list-style-type: none"> • Fertile patches of herb-rich forests • Herb-rich spruce mires
Spruce-mires	Spruce mires and spruce-birch fens	<ul style="list-style-type: none"> • Herb-rich spruce mires
Herb-rich spruce mires	Herb-rich spruce mires	<ul style="list-style-type: none"> • Herb-rich spruce mires

Table 3

Number of patches and total area (ha) of different habitat types in WKHs and reserves for the three study areas.

Biotope	Area 1		Area 2		Area 3	
	WKH sites	Reserves	WKH sites	Reserves	WKH sites	Reserves
<i>Peatlands</i>						
N	53	123	89	82	113	137
Area total	46.2	2738.3	96.2	756.1	88.4	1461.3
<i>Forests</i>						
N	123	309	162	165	355	301
Area total	117.3	2664.0	127.8	1400.6	224.0	2516.7
<i>Heath forests</i>						
N	62	317	74	156	242	286
Area total	69.7	2551.5	78.2	1367.0	155.9	2478.2
<i>Herb-rich forests</i>						
N	25	17	17	3	112	116
Area total	28.3	50.2	17.2	8.0	67.4	312.9
<i>Spruce mires</i>						
N	24	134	10	59	43	163
Area total	27.3	255.8	14.2	180.7	28.9	174.8
<i>Herb-rich spruce mires</i>						
N	24	12	10	0	43	38
Area total	27.3	34.2	14.2	–	28.9	27.0

where n is the total number of patches, a_i and a_j are the sizes of patches i and j , l_{ij} is the number of links in the shortest path between patches i and j , and A_L is the total area of forested land (forests, scrubland and barren land) in the landscape. IIC reaches unity when all of the forested land is occupied by the given habitat type.

IIC is based on a binary connection model, and it treats two patches as connected if a link weight is below a threshold distance and otherwise as unconnected. IIC appreciates the habitat availability concept by integrating the habitat amount and connections between patches in a single measure. This approach recognises that connectivity also happens within a habitat patch, not only between patches. Area-informed indices avoid the ecologically counterintuitive outcome that network connectivity increases with the number of patches, irrespective of the total patch area.

In addition to the overall network evaluation, we calculated patch importance and centrality measures for individual patches. With the patch-level measures we wanted to analyse the role of WKHs in the network based on comparisons between WKH and reserve patches. Patch importance and network centrality measures were calculated at the distance thresholds of 500 m, 1 km, 2.5 km, 5 km, 7.5 km and 10 km. Patch importance values were calculated with the node removal analysis: each patch is systematically removed from the network and the reconstructed network is compared with the original network including the patch. The connectivity loss (per cent) measures the contribution of the patch to the network connectivity. Patch importance values were calculated based on IIC connectivity. We also calculated the per area based importance values by dividing the patch importance value by the patch area. Inferences were based on averaged patch importance values over all the threshold distances.

The network centrality of nodes was evaluated with two measures: degree and betweenness centrality. The degree of a patch equals the number of its direct neighbors. It is a good and simple measure of determining how well a patch is connected to other patches at a local scale (Estrada and Bodin, 2008).

The betweenness centrality of a patch is the proportion of the shortest paths (based on topological distance) between all pairs of patches which run along the patch. For patch x_i the betweenness centrality is calculated as

$$C_B(x_i) = \sum_{j < k}^n \sum_{j < k}^n b_{jk}(x_i)$$

where $b_{jk}(x_i)$ is the proportion of the shortest paths linking x_j and x_k that contain x_i and $i \neq j \neq k$ (according to Freeman et al. (1991)). The contribution of a patch to the large-scale connectivity of the landscape increases with the betweenness centrality measure (Estrada and Bodin, 2008). Betweenness centrality can be used to point out the patches that are located in critical positions relative to other patches from the point of view of a functional network, and has been used to identify stepping stone patches in a patch network. If these critical patches (cut-nodes in graph terminology) were removed, the network would risk being dissected into isolated groups of patches.

We confined our analyses to top-ranking patches in betweenness centrality, because low to intermediate centrality scores do not necessarily hold any meaningful information about the role of the patch in the network (Estrada and Bodin, 2008). We calculated the average for betweenness centrality over all the threshold distances. The patches with an average value >0.01 were designated as top-patches. To check if WKHs contribute to betweenness centrality more than expected by chance, we calculated the probability of finding k WKH patches among n top-patches based on binomial distribution with the following formula:

$$P(X = k) = (n; k)p^k(1 - p)^{n-k}$$

where p is the proportion of WKH patches in a network.

Graphs were analysed with Conefor Sensinode v.2.2 (Saura and Torné, 2009) and Pajek v.1.23 (de Nooy et al., 2005).

3. Results

The patch sizes in reserves were generally consistently larger than those in WKHs (Appendix A). The differences were not so marked, however, for fertile and rare habitat types (e.g. herb-rich forests, spruce mire, herb-rich spruce mires). The difference was even reversed for spruce mires in Area 2. In Area 2 herb-rich spruce mires only occurred in WKHs.

The influence of threshold distance on connectivity was evident in all the results. Networks experienced radical changes with increasing threshold distance; they were mainly composed of isolated patches at small threshold distances, whereas at larger distances they mainly occurred as one component with multiple pathways between patches (Fig. 2).

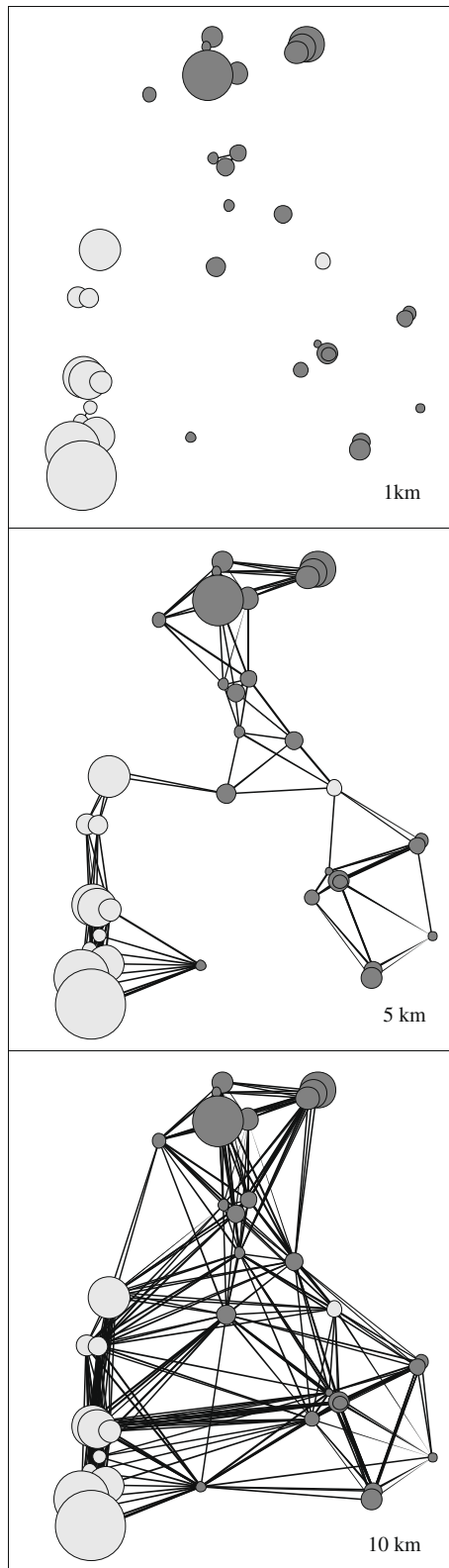


Fig. 2. The herb-rich forest network of Area 1. WKHs (in pale grey) and other reserves (in dark grey) are shown as spheres proportional to their patch sizes. This is a complete graph presentation of the habitat network, where the connections between patches are thresholded at link weights of 1 km, 5 km and 10 km.

For all habitat types, the connectivity of the network in Area 2 was remarkably lower than in other areas (Fig. 3.) Area 3 exceeded other areas in connectivity for forest habitats, whereas Area 1 had

the highest connectivity for peatlands and spruce mires. The enhancement in connectivity from WKHs varied according to the threshold distance and among areas as well as habitat types (Fig. 3). This becomes evident when looking at the percentage increase in connectivity with increasing threshold distance calculated for all habitat types (Fig. 4). WKHs benefited mostly dispersal-limited species in networks of common habitat types (peatlands, forests, heath forests), for which the connectivity increase brought about by WKHs peaked at about threshold distances ranging from ca. 2 to 5 km. In networks of rare habitat types (e.g. herb-rich forests, spruce mires, herb-rich spruce mires), the relative contribution of WKHs to connectivity peaked at much larger threshold distances. But in sparse networks of rare habitat types, the level of the relative connectivity increase was much higher than in dense networks of common habitat types across all threshold distances (except the very smallest ones). This sparse-dense difference was also evident when different areas were compared with each other. Area 2, with small reserve coverage, gained generally more connectivity from WKHs than the other areas. For example, for the herb-rich forest network in Area 2, WKHs increased the habitat area by over 200%, leading to a connectivity increase of over 600%. For more dense networks, the connectivity increases were not so pronounced. For example, in networks of forests the areal increases of ca. 4–9% yielded connectivity increases of ca. 20–50%.

The efficiency of WKH-based conservation was highly dependent on the threshold distance. The proportion of the connectivity contributed by WKHs was smaller than their areal proportion (i.e., the proportion of WKHs of total network area) at small threshold distances, but with greater threshold distances the relative contribution exceeded the areal proportion in all cases (Fig. 5; see Appendix B for result summary). The threshold distance at which the relative connectivity contribution exceeded the areal proportion was network-specific, ranging between 1 and 10 km. For example, in the herb-rich forest networks of Areas 1 and 2, efficiency was achieved at the threshold distance of 5 km, whereas the networks of common habitat types reached the efficiency at a smaller threshold distance, for example heath forests at 1–2 km.

At the level of individual patches, the reserves exceeded the WKHs in patch importance values calculated per area unit (Table 4) (area-informed IIC-patch importance values are summarised in Appendix C). The median values for patch importance were in every case larger in reserves than in WKHs. Reserve patches are thus in general more valuable than WKHs, not only because of their larger size, but also due to their favourable configuration. Some small-sized stepping-stone WKHs had high patch importance values per area unit, which in some cases raised the average patch importance values of WKHs to a higher level than in the reserves. For example, the herb-rich forest WKH patches in Areas 2 and 3 contributed, on average, more to network connectivity per area unit than their reserve counterparts. In networks of rare habitat types, the importance of one area unit was higher than in the networks of common habitat types. For example, one hectare patch in the herb-rich spruce mire networks was approximately worth 3% of the overall network connectivity, whereas in the forest network, one hectare patch was worth 0.05–0.1%. Any single WKH patch in a network of rare habitat type may have a notable value, contributing several percent to the whole network connectivity.

Reserve patches had on average more neighbors than WKHs at all threshold distances, and thus were better connected at the local scale. This applied, for example, to herb-rich forests in Area 3 (Fig. 6). Only in the herb-rich forest network in Area 2 did WKHs have on average a higher degree of scores than reserves across all scales. The degree centrality measures are given in Appendix D.

In sparse networks, proportionally more patches scored high in betweenness centrality than in dense ones. Individual patches in

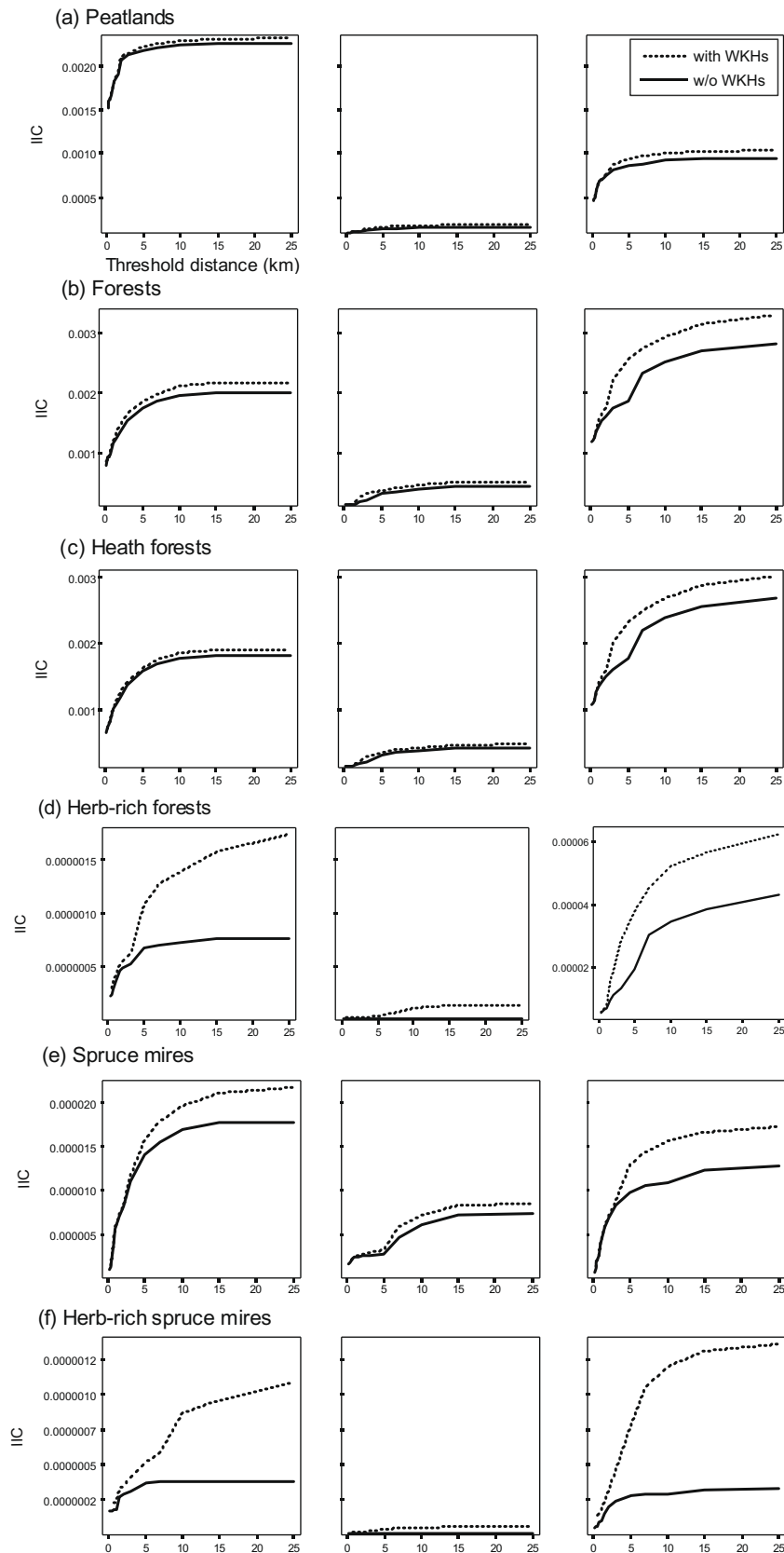


Fig. 3. Overall network connectivity based on the Integral Index of Connectivity (IIC) for different habitat networks as a function of threshold distance (i.e. dispersal ability). Two networks are formed; one without WKHs and another with WKHs.

dense networks did not play such a critical role in betweenness due to numerous alternative connections. The proportion of top-

patches (of the total number of patches in an area) ranged from 2% in the heath forest network (network size 656 patches) of Area

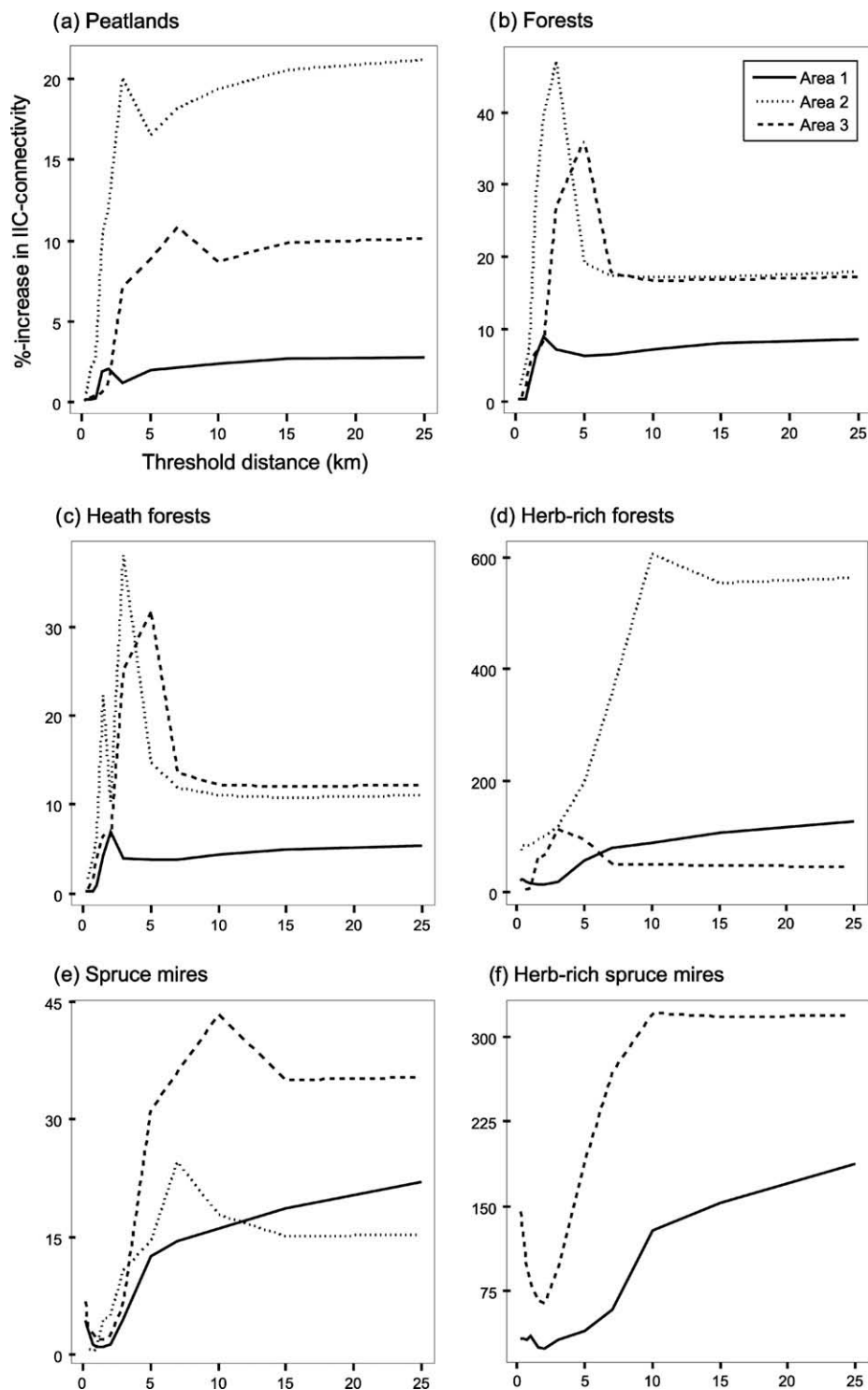


Fig. 4. Increase in IIC connectivity (per cent) brought about by the additions of WKHs to the different reserve networks as a function of threshold distance.

3–55% in the herb-rich forest network (network size 20 patches) of Area 2. The median proportion for top-patches for all area-habitat type network combinations was 11.6%.

In general, top-patches were distributed among reserves and WKHs in direct proportion to their numbers. However, in the forest, spruce mire and herb-rich spruce mire networks of Area 3, there were more WKHs among top-patches than expected by chance ($p = 0.022$, $p = 0.014$ and $p = 0.019$, respectively).

4. Discussion

When analysed from the point of view of a functional network, WKHs seem to be valuable. WKHs did not just contribute to the reserve network in terms of area, but they also created new inter-patch connections. To ensure the availability of habitats that occur naturally scattered in a landscape, WKHs may be a more efficient and straightforward form of conservation than large reserves. We

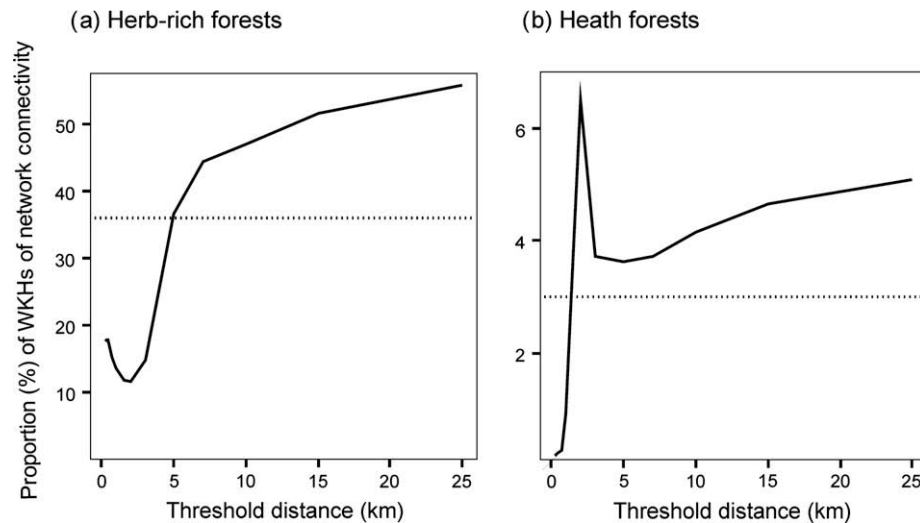


Fig. 5. The proportion (%) of WKHs of overall network connectivity as a function of threshold distance for the herb-rich forest and heath forest network of Area 1. The proportion (%) of WKHs of the total network area is shown with a dashed line. WKHs are an efficient way to increase landscape connectivity when their proportional connectivity contribution exceeds their areal proportion in the network.

Table 4

Patch importance values per area unit (ha) (based on the Integral Index of Connectivity, IIC) compared between WKHs and reserves for three study areas. Results where WKHs have higher average patch importance values per area unit than reserves are in bold.

	Area 1		Area 2		Area 3	
	WKHs	Reserves	WKHs	Reserves	WKHs	Reserves
<i>Peatlands</i>						
Median	0.027	0.054	0.107	0.109	0.049	0.083
Mean \pm SD	0.031 \pm 0.01	0.053 \pm 0.03	0.118 \pm 0.05	0.127 \pm 0.06	0.053 \pm 0.02	0.086 \pm 0.04
<i>Forests</i>						
Median	0.036	0.067	0.073	0.081	0.035	0.068
Mean \pm SD	0.101 \pm 0.01	0.063 \pm 0.47	0.107 \pm 0.18	0.101 \pm 0.05	0.046 \pm 0.06	0.064 \pm 0.02
<i>Heath forests</i>						
Median	0.032	0.073	0.084	0.084	0.038	0.071
Mean \pm SD	0.045 \pm 0.09	0.068 \pm 0.01	0.898 \pm 6.83	0.103 \pm 0.05	0.048 \pm 0.05	0.068 \pm 0.02
<i>Herb-rich forests</i>						
Median	1.174	2.313	4.472	5.320	0.355	0.389
Mean \pm SD	1.416 \pm 0.78	2.319 \pm 0.53	4.576 \pm 1.76	2.319 \pm 1.90	0.424 \pm 0.42	0.406 \pm 0.13
<i>Spruce mires</i>						
Median	0.303	0.714	0.525	1.069	0.445	1.114
Mean \pm SD	0.369 \pm 0.27	0.750 \pm 0.34	0.625 \pm 0.21	0.919 \pm 0.53	0.449 \pm 0.12	1.088 \pm 0.46
<i>Herb-rich spruce mires</i>						
Median	1.440	2.989	10.532	–	2.355	3.705
Mean \pm SD	3.214 \pm 5.20	2.811 \pm 0.61	10.368 \pm 2.24	–	3.340 \pm 4.14	3.773 \pm 1.62

suggest that WKHs provide a means to supplement the nature reserve network in rare and scattered habitat types. This was evident particularly for herb-rich forests and herb-rich spruce mires. Large continuous forest reserves do not provide area or connectivity for these habitat types, and WKHs are definitely needed both to increase habitat availability and to promote the dispersal of species specialised in such habitat types.

The efficiency of the WKH-based conservation depended greatly on the dispersal abilities of species. For species with weak dispersal capabilities, WKHs are not likely to be an optimal way of providing habitat, but larger set-asides would be a more efficient solution. For species with good dispersal capabilities, WKH-based conservation seems to be efficient when analysed from the network perspective. For these species the WKHs are also bridging habitats in reserves that would otherwise remain unconnected, and thus increase habitat availability over their own areal proportion. There is no specific limit for the dispersal capacity above which the

WKH would prove to be efficient; instead, the outcome is dependent on the characteristics of the network. For species requiring more rare and scattered habitat types, a greater dispersal capacity is required in order for them to benefit from the contribution of WKHs to connectivity than for species requiring more common habitat types.

The result of our study, i.e., that the networks were in general considerably more connected with than without WKHs, points to the value of WKHs at the level of the whole network, not at the level of individual WKHs. Reserve patches were generally larger in size and more strategically located than WKHs. It is the combined effect of all the WKHs together with reserves that makes them valuable in the network. The relatively high density of WKHs is the most likely reason for their value in the network as a whole. However, WKHs among the top-patches in between centrality indicate that some individual WKHs are also important in sustaining the large-scale connectivity of the networks. Without WKHs,

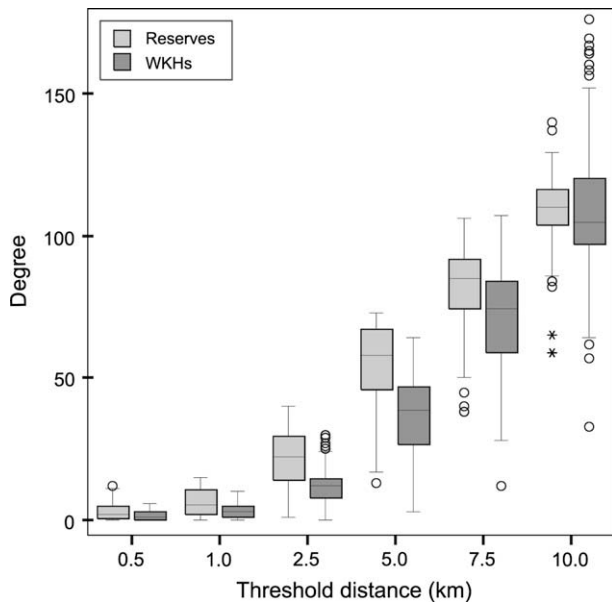


Fig. 6. Comparisons of degree centrality measures between WKHs and reserves for the herb-rich forest patches in Area 3 at threshold distances ranging from 0.5 km to 10 km.

dispersing individuals would experience the network as more fragmented.

The coverage of the reserve network in Area 2 is closest to the typical level in Southern Finland, although somewhat above the average. The share of WKHs in Area 2 represents the average level in Central Finland and is ca. 0.1% lower than in Southern Finland as a whole. In our study, Area 2 exemplified an area with a sparse reserve network, and in this area the connectivity of the reserve network was greatly enhanced by WKHs. This reflects the potentially important role of WKHs as part of the reserve network in Southern Finland. In regions with substantially greater reserve coverage, the WKH-based conservation most likely serves species that are highly dispersal-limited. The results from Area 3 indicate that the high density of WKHs increases the value of WKH-based conservation. This is most evident when comparing the results from Area 1 and Area 3 which cover approximately the same reserve area while WKHs are more numerous in Area 3.

The target species of WKHs are red-listed species with small areal demands, mainly bryophytes, invertebrates (though very poorly studied), lichens, polypores, and vascular plants. Empirical evidence suggests that WKHs may be biodiversity hotspots for epiphytic lichens (e.g. Johansson and Gustafsson, 2001; Pykälä, 2004) and rare bryophytes (Perhans et al., 2007; but see Gustafsson et al., 2004), but not necessarily for polypore fungi (Sippola et al., 2005). Dispersal has been considered a limiting factor for many threatened forest species, which call for spatial considerations in their protection (see Edman et al. (2004a) and Penttilä et al. (2006) for polypores; Sillett et al. (2000) and Johansson and Ehrlén (2003) for epiphytic lichens).

The dispersal capacities of threatened forest species are poorly known, and thus we cannot draw firm conclusions about how large a proportion of the red-listed species are good enough dispersers to gain benefit from the enhanced connectivity provided by the WKHs. Our range of threshold distances (from 200 m to 25 km) is based on the dispersal estimates for threatened forest beetles, as they represent the extremes of reported dispersal abilities for threatened forest biota. The maximum detected dispersal distance of a hollow-tree specialist *Osmoderma eremita* was found to be 190 m (Ranius and Hedin, 2001), whereas Jonsson (2003) recorded

a median dispersal distance of 12 km and a maximum distance of 28.7 km for the saproxylic beetle *Oplocephala haemorrhoidalis* in a flight-mill experiment. When more information on species dispersal distances becomes available, our results can be interpreted a posteriori for any given threatened species with an estimate of its dispersal ability. It is worth noting that a functional reserve network cannot be based on extreme dispersal events. For example, although the individual airborne spores of polyporous fungi can travel very long distances, the successful colonisation (requiring large number of spores) of polypore species has been suggested to be dispersal-limited (Edman et al., 2004a,b). Thus, it is important that the dispersal ability estimates used for interpretations are ecologically realistic and not overly optimistic.

To be functionally connected, reserve networks (even with WKHs) place great demands on the dispersal ability of organisms. If a species' maximum dispersal distance is 3 km, all habitat type networks are unconnected (based on IIC). Networks of peatlands, forests and heath forests are very close to being connected with this threshold distance, but individuals would still perceive the other networks disconnected. It seems that the sparser networks are too fragmented for dispersal-limited forest species. The WKH patches considerably increased the connectivity of the sparse networks, but the increase in connectivity benefits most the species with a good dispersal ability (up to 5 km). It is kilometres that matter in these networks, not hundreds of metres. For poor dispersers, the networks with or without WKHs consist mainly of isolated patches.

The binary approach to a landscape consisting of a matrix surrounding the suitable "islands" of habitat patches is appropriate for the species that perceive the matrix as predominantly hostile. Many red-listed species have such specific habitat requirements (for example, those requiring a shady microclimate or a high density of dead-wood) that they cannot easily be fulfilled in production forests. The degree to which the reserves are functionally linked by dispersal becomes increasingly important for those specialised forest species. By contrast, the species for which the matrix also provides habitats and resources, perceive the landscape as a more gradually varying entity of different resource densities. For such species, our analysis may severely underestimate habitat availability and landscape connectivity.

In our study, the distances between patches were calculated as Euclidean distances. As the target species of WKHs mainly disperse by airborne spores and seeds, a geographical distance is a good approximation of the inter-patch distance experienced by an organism. For those species that use insect vectors or active movement (shaped by the matrix) for their dispersal, the straight-line distance may underestimate the effective distance between patches.

We analysed the value of WKHs only from the habitat connectivity perspective. There are also other things that need to be considered to determine the ultimate value of WKHs in the conservation of threatened species. There are many qualitative problems in setting aside small forest parcels embedded in a managed forest matrix. Many of the problems are directly related to the small size of the WKHs. Our study was conducted on the assumption that WKHs contribute to connectivity worth their habitat area. Ecological processes are, however, usually weighted down in small patches surrounded by an intensively managed matrix, so the habitat area does not necessarily equal the ecological value. The smaller the patch is, the greater the influence external factors are likely to have on the microclimatic conditions (Saunders et al., 1991). According to a study by Aune et al. (2005) most of the small-sized WKHs totally lack core area. The areas of WKHs based on official delimitations may be too optimistic, especially from the point of view of species that are sensitive to microclimatic conditions.

Small WKH sites can host only small populations, and thus the populations in WKHs are prone to extinctions (e.g. Hansson, 2001). Pykälä (2004) found in his monitoring study on epiphytic macrolichens that although concentrated in WKHs, their small population sizes predisposed them to local extinctions in less than 10 years. The long term occurrence of species in WKHs may thus depend on repeated colonisation to compensate for local extinctions. Colonisation rate has been shown to depend on the isolation of a patch (e.g. Verboom et al., 1991). The immigration of individuals to a small population may save that population from extinction (called ‘the rescue effect’) (Brown and Kodric-Brown, 1977). The rescue effect, and thus also extinction risk, is also related to the isolation of patches as the possible immigration diminishes with increasing distance from the other occupied patches. The configuration of suitable patches may thus be a critical issue for the viability of populations residing in WKHs. In our study, we evaluated the connectivity contributions of WKHs from the point of view of the reserve network, but the traditional reserve network is likewise a prerequisite for successful WKH-based biodiversity protection.

Finnish legislation allows cautious selective logging in WKHs as long as site features are not destroyed or altered. This may cause reductions in ecological values, a decrease in the amount of dead wood in long term, for example. Selective logging can also change the microclimatic conditions and make them unsuitable for most sensitive species. Pykälä (2004) found that logging in WKHs was the main cause of extinctions in epiphytic macrolichens. To sustain population persistence and to augment the existing reserve network, it is important that WKHs maintain their habitat qualities. It may be necessary to refrain from any logging in WKHs. Similarly, a buffer zone around WKHs would give protection against the detrimental effects that a surrounding matrix exerts on WKHs. For example, 30-m buffer zones have been found adequate to maintain the original species composition in riparian WKH sites (Selonen and Kotiaho, 2006).

It has been suggested that there is a threshold value of habitat availability below which the effect of habitat patterns on population persistence may become evident (Andrén, 1994). For example, Andrén (1994) reported an empirical threshold value of 10–30% of habitat availability for birds and mammals. The threshold value is species- and landscape-context-specific and supposedly higher for species dispersing less well than birds and mammals (Mönkkönen and Reunanen, 1999). As the coverage of reserves in Finland apparently falls below any critical threshold, the configuration of reserves in the landscape is important for the persistence of many threatened forest species. Thus, WKHs have a potentially important role in providing connectivity for species for which production forests are unsuitable.

The importance of reserve configuration is scale dependent. For organisms that perceive the landscape at fine scales, landscape configuration is of little consequence, because populations are restricted to local habitat patches (Keitt et al., 1997). For these poor dispersers the importance of a reserve is thus largely determined by its size. Likewise, landscape configuration is likely to be of minor importance for species capable of traversing long distances across hostile landscapes. In contrast, species with a dispersal ability within a critical threshold range (i.e. the range where a small change in dispersal ability produces a great change in connectivity) experience the importance of spatial configuration the most (Keitt et al., 1997). WKHs shift the critical threshold range towards lower threshold distances, and species with a dispersal ability within this range shift are the ones that WKH-based conservation serves the best. As the critical threshold range is network-specific (for common habitat types occurring at lower threshold distances than for rare habitat types), the benefits associated with any given dispersal ability vary among different networks.

We suggest that WKH-based conservation would bring the greatest benefits in landscapes with a rather low habitat availability. Thus, setting aside WKHs would seem to be a more efficient and well-founded conservation tool in landscapes with intensive land use and forest management history. By contrast, we see little value in WKHs in landscapes where habitat availability is still at a high level for most species. However, in landscapes with a very low habitat availability and a highly fragmented habitat network, WKH-based conservation may not serve dispersal-limited species but only efficient dispersers instead. The benefits of WKH-based conservation can be evaluated in the light of the landscape context and the dispersal abilities of the species.

5. Conclusions

The smaller the land parcels we are setting aside, the more important the issue of functional connectivity becomes. New approaches are needed that deal explicitly with the spatial arrangement of the reserves in order to form ecologically sustainable and functional networks. To effectively maintain biodiversity through time, a reserve network needs to be designed and evaluated with explicit consideration to the reserve configuration. Woodland key habitats have been criticised as being too small and scattered in distribution. However, WKHs are not detached conservation elements in the forest landscape. We argue that they form a network with other reserves, and their real ecological value can only be understood as an integral part of the network.

Our main aim here was to evaluate the importance and role of WKHs within the reserve network. Our results show that, especially for species requiring fertile habitat types that occur naturally scattered in the forest landscape, WKH-based conservation can be very valuable. The value of setting aside WKHs is strongly linked with the dispersal ability of threatened species. It is evident in our analysis that the protection of large set-asides would be a more efficient conservation strategy for species with weak dispersal abilities. From the perspective of the functional connectivity in the protected-area network, the whole is clearly more than the sum of its constituent parts. Network connectivity is an emergent property that can only be understood at the level of the whole network.

Finally, even though we found that WKHs are important from the connectivity perspective, we note that the conservation of small-sized WKHs surrounded by an intensively managed forest matrix does also have its pitfalls. Most importantly, the site characteristics of WKHs must be safeguarded for them to be able to contribute to the connectivity of the reserve network. The deleterious effects of selective logging should be prevented in the first place. Buffer zones around WKHs would also moderate the edge effects from the surrounding matrix on WKH sites. On these conditions, WKHs seem to have the potential to contribute to network connectivity up to the level shown in our study.

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Finland) for contacting the landowners and to all landowners who let us to use information on their property in this study.

Appendix A

Mean (\pm SD) and median patch sizes of different habitat types in WKHs and reserves for three study areas.

Biotope	Area 1		Area 2		Area 3	
	WKH sites	Reserves	WKH sites	Reserves	WKH sites	Reserves
<i>Peatlands</i>						
Mean patch size \pm SD	0.87 \pm 0.75	22.26 \pm 119.03	1.08 \pm 1.68	9.22 \pm 43.43	0.78 \pm 1.27	10.67 \pm 59.53
Md for patch size	0.59	1.53	0.63	1.82	0.43	0.95
<i>Forests</i>						
Mean patch size \pm SD	0.95 \pm 1.43	8.62 \pm 31.69	0.79 \pm 1.08	8.49 \pm 27.43	0.63 \pm 0.95	8.36 \pm 38.50
Md for patch size	0.58	1.07	0.41	1.00	0.34	0.57
<i>Heath forests</i>						
Mean patch size \pm SD	1.12 \pm 1.50	8.05 \pm 24.46	1.06 \pm 1.21	8.76 \pm 27.54	0.64 \pm 0.86	8.66 \pm 34.01
Md for patch size	0.68	1.07	0.63	1.05	0.37	0.62
<i>Herb-rich forests</i>						
Mean patch size \pm SD	1.13 \pm 1.40	2.95 \pm 3.57	1.01 \pm 0.80	2.67 \pm 3.11	0.60 \pm 0.94	2.70 \pm 6.60
Md for patch size	0.77	1.18	0.81	0.95	0.33	0.77
<i>Spruce mires</i>						
Mean patch size \pm SD	1.14 \pm 1.43	1.91 \pm 2.51	1.42 \pm 0.77	3.06 \pm 5.68	0.67 \pm 1.15	1.07 \pm 1.62
Md for patch size	0.75	1.10	1.42	1.31	0.38	0.60
<i>Herb-rich spruce mires</i>						
Mean patch size \pm SD	1.14 \pm 1.43	2.85 \pm 3.33	1.42 \pm 0.77	–	0.67 \pm 1.15	0.71 \pm 0.84
Md for patch size	0.75	1.23	1.42	–	0.38	0.47

Appendix B

The proportion (%) of WKHs of total network area and of overall network connectivity at different threshold distances. Results were WKH have higher network connectivity than their areal proportion are in bold.

	Area 1	Area 2	Area 3
<i>Peatlands</i>			
Area	1.66	11.29	5.71
Overall			
200 m	0.11	0.32	0.10
1 km	0.27	2.72	0.37
2 km	2.04	9.26	1.10
3 km	1.18	16.75	6.64
5 km	1.96	15.37	8.16
10 km	2.30	16.23	8.04
25 km	2.67	17.49	9.19
<i>Forests</i>			
Area	4.22	8.36	8.17
Overall			
200 m	0.24	1.78	0.16
1 km	2.51	7.22	4.97
2 km	8.14	28.27	7.41
3 km	6.71	32.04	21.27
5 km	5.85	16.08	26.58
10 km	6.76	14.68	14.31
25 km	7.89	15.14	14.75
<i>Heath forests</i>			
Area	2.66	5.41	5.92

Appendix B (continued)

	Area 1	Area 2	Area 3
Overall			
200 m	0.17	1.34	0.11
1 km	0.90	6.13	3.75
2 km	6.50	9.37	5.87
3 km	3.73	27.60	19.98
5 km	3.73	12.86	24.18
10 km	4.16	9.94	10.84
25 km	5.08	9.92	10.92
<i>Herb-rich forests</i>			
Area	36.00	68.22	17.72
Overall			
200 m	17.64	40.48	2.40
1 km	13.47	45.91	7.30
2 km	11.62	49.63	39.16
3 km	14.84	54.06	53.11
5 km	36.54	66.28	48.54
10 km	47.00	85.83	33.46
25 km	55.75	84.95	31.10
<i>Spruce mires</i>			
Area	9.64	7.26	14.20
Overall			
200 m	4.23	0.59	6.97
1 km	1.02	0.67	1.91
2 km	1.35	4.79	2.44
3 km	4.39	9.81	6.09
5 km	11.11	12.63	23.76
10 km	13.92	15.21	30.23
25 km	18.02	13.22	26.13
<i>Herb-rich spruce mires</i>			
Area	44.37	100	51.73
Overall			
200 m	24.04	–	59.84
1 km	25.42	–	44.45
2 km	18.90	–	38.71
3 km	23.52	–	48.63
5 km	27.83	–	65.34
10 km	56.27	–	76.27
25 km	65.22	–	76.16

Appendix C

Patch importance values (based on Integral Index of Connectivity, IIC) compared between WKHs and reserves for three study areas.

	Area 1 WKHs	Area 2 Reserves	Area 3 WKHs	Reserves	WKHs	Reserves
<i>Peatlands</i>						
Min–max	0.002–0.081	0.001–63.329	0.007–1.020	0.006–83.617	0.001–0.540	0.001–78.033
Median	0.018	0.084	0.071	0.176	0.022	0.076
Mean ± SD	0.025 ± 0.02	1.286 ± 7.05	0.118 ± 0.14	1.719 ± 9.34	0.042 ± 0.07	1.102 ± 6.84
Sum	1.326	158.23	10.479	140.945	4.753	150.979
<i>Forests</i>						
Min–max	0.000–0.361	0.001–29.442	0.002–0.878	0.002–44.115	0.001–0.302	0.009–39.958
Median	0.022	0.067	0.029	0.095	0.014	0.031
Mean ± SD	0.039 ± 0.059	0.619 ± 2.549	0.073 ± 0.116	1.026 ± 4.022	0.027 ± 0.041	0.587 ± 3.172
Sum	4.858	191.121	11.756	169.304	9.587	176.631

(continued on next page)

Appendix C (continued)

	Area 1 WKHs	Area 2 Reserves	Area 3 WKHs	Reserves	WKHs	Reserves
<i>Heath forests</i>						
Min–max	0.001–0.317	0.001–17.438	0.003–2.599	0.002–46.054	0.001–0.254	0.001–30.841
Median	0.022	0.070	0.055	0.100	0.016	0.038
Mean ± SD	0.042 ± 0.06	0.615 ± 2.06	0.147 ± 0.33	1.104 ± 4.28	0.030 ± 0.04	0.640 ± 2.89
Sum	2.584	194.966	10.849	172.302	7.211	182.933
<i>Herb-rich forests</i>						
Min–max	0.212–10.632	0.715–42.583	0.172–15.557	2.414–42.583	0.007–2.716	0.004–36.847
Median	0.873	1.900	4.174	5.070	0.116	0.310
Mean ± SD	1.682 ± 2.28	7.530 ± 10.51	5.377 ± 5.21	16.689 ± 22.46	0.223 ± 0.36	1.245 ± 3.74
Sum	42.049	128.016	91.407	50.067	24.991	144.408
<i>Spruce mires</i>						
Min–max	0.057–1.963	0.031–16.549	0.167–2.379	0.027–49.613	0.008–3.963	0.009–13.605
Median	0.252	0.775	0.637	0.933	0.159	0.622
Mean ± SD	0.345 ± 0.39	1.430 ± 1.20	0.890 ± 0.66	2.812 ± 6.74	0.322 ± 0.61	1.137 ± 1.70
Sum	8.286	191.671	8.895	165.914	13.832	185.366
<i>Herb-rich spruce mires</i>						
Min–max	0.255–14.892	0.954–43.492	1.379–29.260	–	0.033–27.031	0.030–3.194
Median	1.160	3.024	12.568	–	0.867	1.427
Mean ± SD	2.557 ± 3.26	9.064 ± 12.12	15.276 ± 9.24	–	2.122 ± 4.19	2.633 ± 3.19
Sum	61.36	108.765	152.764	–	91.225	100.040

Appendix D

Means (±SD) for degree centrality measure of different habitat types in WKHs and reserves for three study areas. Results where WKHs have higher average degree scores than reserves are in bold.

	Area 1 WKHs	Area 2 Reserves	Area 3 WKHs	Reserves	WKHs	Reserves
<i>Peatlands</i>						
500 m	1.1 ± 1.6	5.2 ± 5.3	1.2 ± 1.2	2.2 ± 2.2	2.2 ± 2.6	4.8 ± 3.4
1 km	2.7 ± 3.0	10.4 ± 7.4	3.2 ± 3.0	4.2 ± 3.2	5.5 ± 5.7	10.2 ± 5.2
2.5 km	10.2 ± 8.9	32.9 ± 16.8	11.7 ± 7.5	12.1 ± 7.0	17.8 ± 15.2	34.3 ± 13.0
5 km	30.7 ± 24.6	70.1 ± 24.4	34.4 ± 15.0	33.3 ± 12.7	44.8 ± 21.4	80.6 ± 19.9
7.5 km	54.7 ± 39.0	100.1 ± 25.3	58.6 ± 19.1	62.2 ± 20.3	81.1 ± 28.8	117.1 ± 19.8
10 km	83.1 ± 50.1	126.7 ± 21.4	82.7 ± 21.9	89.2 ± 25.1	125.5 ± 40.8	149.2 ± 24.7
<i>Forests</i>						
500 m	1.5 ± 1.5	8.1 ± 6.2	1.3 ± 1.4	4.9 ± 4.5	3.2 ± 2.1	4.7 ± 3.6
1 km	3.9 ± 3.0	17.8 ± 10.5	3.4 ± 3.0	9.4 ± 7.5	9.2 ± 4.5	10.2 ± 6.2
2.5 km	18.8 ± 14.9	59.7 ± 24.7	15.3 ± 8.1	23.8 ± 12.33	37.8 ± 16.3	37.6 ± 19.4
5 km	61.38 ± 42.1	146.6 ± 48.9	49.5 ± 19.6	62.0 ± 21.42	110.3 ± 29.4	107.7 ± 40.9
7.5 km	124.4 ± 75.9	223.2 ± 64.3	92.98 ± 31.2	104.7 ± 28.0	184.0 ± 32.4	198.9 ± 63.0
10 km	203.6 ± 114.1	295.9 ± 63.4	139.3 ± 46.0	155.4 ± 38.37	271.1 ± 49.1	306.0 ± 80.8
<i>Heath forests</i>						
500 m	1.2 ± 1.5	8.4 ± 6.1	1.2 ± 1.4	4.8 ± 4.7	2.9 ± 2.2	7.3 ± 5.2
1 km	2.8 ± 2.7	18.4 ± 10.8	3.2 ± 3.5	9.0 ± 7.9	6.7 ± 3.8	17.5 ± 11.4
2.5 km	12.1 ± 12.1	62.3 ± 28.2	12.6 ± 9.2	20.4 ± 13.6	25.9 ± 11.6	61.7 ± 28.0
5 km	41.0 ± 35.2	149.3 ± 55.1	41.0 ± 22.3	49.1 ± 23.8	79.8 ± 35.0	152.6 ± 50.6
7.5 km	83.2 ± 67.8	217.5 ± 67.2	71.9 ± 30.2	76.9 ± 26.3	150.4 ± 58.8	234.0 ± 61.1
10 km	143.3 ± 108.9	275.9 ± 60.5	103.2 ± 36.4	112.1 ± 32.1	226.6 ± 75.5	295.8 ± 62.9
<i>Herb-rich forests</i>						
500 m	0.6 ± 0.9	1.2 ± 1.0	0.4 ± 0.5	0.0 ± 0.0	1.6 ± 1.6	3.1 ± 3.0
1 km	1.2 ± 0.9	2.0 ± 1.1	1.4 ± 1.4	0.7 ± 0.6	3.6 ± 2.5	6.3 ± 4.7
2.5 km	2.1 ± 1.2	4.2 ± 2.3	1.3 ± 1.4	0.7 ± 0.6	12.1 ± 6.6	21.7 ± 9.8
5 km	6.4 ± 1.4	9.6 ± 3.1	3.0 ± 2.6	1.7 ± 1.2	37.4 ± 14.5	54.0 ± 14.6
7.5 km	11.6 ± 2.6	12.9 ± 1.9	5.8 ± 3.0	5.3 ± 5.1	71.5 ± 20.0	82.6 ± 14.5
10 km	15.5 ± 4.8	17.3 ± 3.5	8.1 ± 3.5	7.3 ± 4.5	108.8 ± 26.4	109.0 ± 13.4

Appendix D (continued)

	Area 1 WKHs	Area 2 Reserves	Area 3 WKHs	Reserves	WKHs	Reserves
<i>Spruce mires</i>						
500 m	0.7 ± 0.9	3.3 ± 2.3	0.6 ± 0.5	3.3 ± 2.9	0.9 ± 1.1	5.9 ± 4.2
1 km	1.3 ± 0.8	7.6 ± 4.6	0.7 ± 0.5	6.8 ± 5.4	1.6 ± 1.4	15.9 ± 10.8
2.5 km	3.7 ± 1.7	29.0 ± 15.4	5.5 ± 4.3	16.4 ± 12.5	4.8 ± 3.1	54.7 ± 29.5
5 km	14.4 ± 10.7	68.7 ± 26.7	20.4 ± 11.8	23.8 ± 14.9	18.6 ± 8.0	105.1 ± 35.0
7.5 km	29.4 ± 21.1	95.8 ± 27.9	36.9 ± 11.2	30.0 ± 15.2	43.7 ± 20.9	134.4 ± 31.6
10 km	55.5 ± 41.9	119.1 ± 23.3	42.8 ± 11.0	36.8 ± 15.3	80.3 ± 43.3	150.8 ± 32.3
<i>Herb-rich spruce mires</i>						
500 m	0.7 ± 0.9	1.2 ± 1.1	–	–	0.8 ± 1.1	2.0 ± 1.7
1 km	0.7 ± 0.9	1.2 ± 1.1	–	–	1.5 ± 1.4	5.0 ± 3.8
2.5 km	2.2 ± 1.1	4.0 ± 1.7	–	–	3.9 ± 2.6	14.1 ± 7.3
5 km	6.0 ± 1.5	9.3 ± 2.2	–	–	12.6 ± 6.7	28.9 ± 6.4
7.5 km	10.2 ± 2.1	10.7 ± 1.7	–	–	24.5 ± 8.5	36.5 ± 4.5
10 km	13.6 ± 3.5	14.5 ± 2.1	–	–	40.6 ± 12.1	46.3 ± 6.0

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