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Woodpecker assemblages in natural and managed boreal and hemiboreal forest — a review

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Woodpecker species as a group require several properties (dead wood, old deciduous and large trees) that are characteristic of natural forest, the presence of which are not compatible with intensive forest management. The occurrence of many woodpecker species may thus indicate a high degree naturalness of forests. Using woodpeckers as indicators requires that we understand how these species were distributed in naturally dynamic landscapes, as well as quantitative knowledge of their requirements. We review the basic biology of boreal/hemiboreal woodpeckers and compare the degree of specialization of the different woodpecker species with their population trends and with changes in habitat distribution in the boreal/hemiboreal landscape over the last century. The comparison shows that there is a close connection between the degree of specialization of woodpeckers, the changes in forests and recent population trends. Thus woodpecker species as a group are in conflict with intensive forest management. To keep viable populations of all woodpecker species in a landscape existing values must be preserved and natural features be built into future forests. Future research should include studies of distribution, abundance, habitat niche breadth and fitness of different woodpecker species in landscapes with different degrees of naturalness.

1. Introduction

For centuries the expansion of agriculture and forest management has altered the extent and pattern of forest cover in the landscape in northern Europe, as well as the structure of the forest habitats themselves, (Thirgood 1989, Angelstam in press). Also, even if the forest cover, and wood volume in stands, is similar to or higher than in the natural conditions, the distribution and amount of different structural components and the function of important processes have been altered (Gamlin 1988, Angelstam 1992, Esseen et al. 1992, Linder & Östlund 1992). As a consequence of reduction of dead and decaying wood, old and large trees, and forests with a long continuity under forest cover, 1487 species of plants and animals have been classified in the Swedish "Red lists" (Berg et al. in press). Many of these important properties are typical for older successional stages of forests and

for forests with internal dynamics that have a low net production of wood.

Birds respond rapidly to changes in habitat and landscape structures. The pattern in Fennoscandia is that resident species depending on old successional stages have declined while migrant species preferring clearcuts or young forests have shown a corresponding increase (Järvinen et al. 1977, Järvinen & Väisänen 1977, Väisänen et al. 1986). These changes have to a great extent been explained by a change in the age structure of forest, particularly due to loss of old boreal forest stands (Haila et al. 1980, Helle & Järvinen 1986, Boström 1988). Also other aspects of forest quality have been used to explain the differences in bird species richness and composition found in similar successional stages. In a landscape dominated by coniferous forest, the amount of dead wood (Haapanen 1965, Järvinen et al. 1977, Haila et al. 1987, Niemi & Hanowski 1984) and the density of deciduous trees (aspen, *Populus tremula*, and birches, *Betula* spp.) (Angelstam 1992, Stenberg & Hogstad 1992) has been found to influence the composition and species richness of especially resident bird species.

To understand how altered distribution and juxtaposition of stands with different properties influence wildlife species, the woodpecker species as a group is good for detailed analyses since this is the most demanding group among the resident bird species (Ahlén 1975a, Cramp 1985, Wesołowski & Tomiałojć 1986, Short & Horne 1990, Angelstam 1990, 1992). By demanding we mean that these species are dependent on properties, the presence of which are in strong conflict with traditional forest management; several species forage in dead wood and breed in old deciduous trees. Moreover, due to their large body size, they need large areas with old-growth properties, but can also add up a set of discrete dispersed patches to an acceptable area. Hence, woodpeckers use a landscape rather than a single patch of one habitat type. Their presence may thus be used as an indication of the degree of reductions of properties that have caused many other animal and plant species to become endangered in areas where forest management has been too intense (Rassi & Väisänen 1987, Ahlén & Tjernberg 1992, Berg et al. in press). In conifer-dominated Old World forests this applies especially to the white-backed woodpecker *Dendrocopos leucotos* and the lesser spotted woodpecker *Dendrocopos minor* found in forests with old deciduous trees (Wesołowski & Tomiałojć 1986, Aulén 1988, Cramp 1985, Nilsson & Pettersson 1990, Wiktander et al. 1992), but also to the three-toed woodpecker *Picoides tridactylus* (Wesołowski & Tomiałojć 1986), which usually is found in old coniferous forest.

The more generalistic species the great spotted woodpecker *Dendrocopos major* and the black woodpecker *Dryocopus martius* are less sensitive to the structural changes in forests, and are not endangered. However, since these species are the most important primary nest hole excavators, they may be viewed as important key-stone species for nest hole production (Johnsson et al. 1990, Johnsson 1993). Therefore, even changes in density or in the ranges of these species may be of importance at a community level.

In Sweden there is presently an agreement that forest management should mimic the natural disturbance regimes of forests (Pettersson 1991, Liljelund et al. 1992, SOU 1992, Angelstam et al. 1993). As human-caused alteration of forest landscape has already continued for a long time, it may be difficult to ascertain what is a good habitat for a given species. Studies on habitat selection may not be relevant since the range of possible habitats is restricted in the managed landscape due to past losses of certain quality aspects. In other words, the range of habitat characteristics we can sample in a managed landscape may be too narrow to permit sound conclusions about how natural woodpecker assemblages are composed. For the reconstruction of important properties it is therefore important to understand how species were distributed in naturally dynamic landscapes. This applies in particular to woodpeckers as potential indicator and key-stone species.

In this paper we review woodpecker food and feeding site as well as nest site selection and the degree of residency. We also compare the degree of specialization of the different woodpecker species with the population trends of these species and with changes in habitat distribution in the boreal/hemiboreal landscape over the last century. As a starting point we review the present knowledge and ideas about the landscape and habitat composition of the pristine boreal/hemiboreal

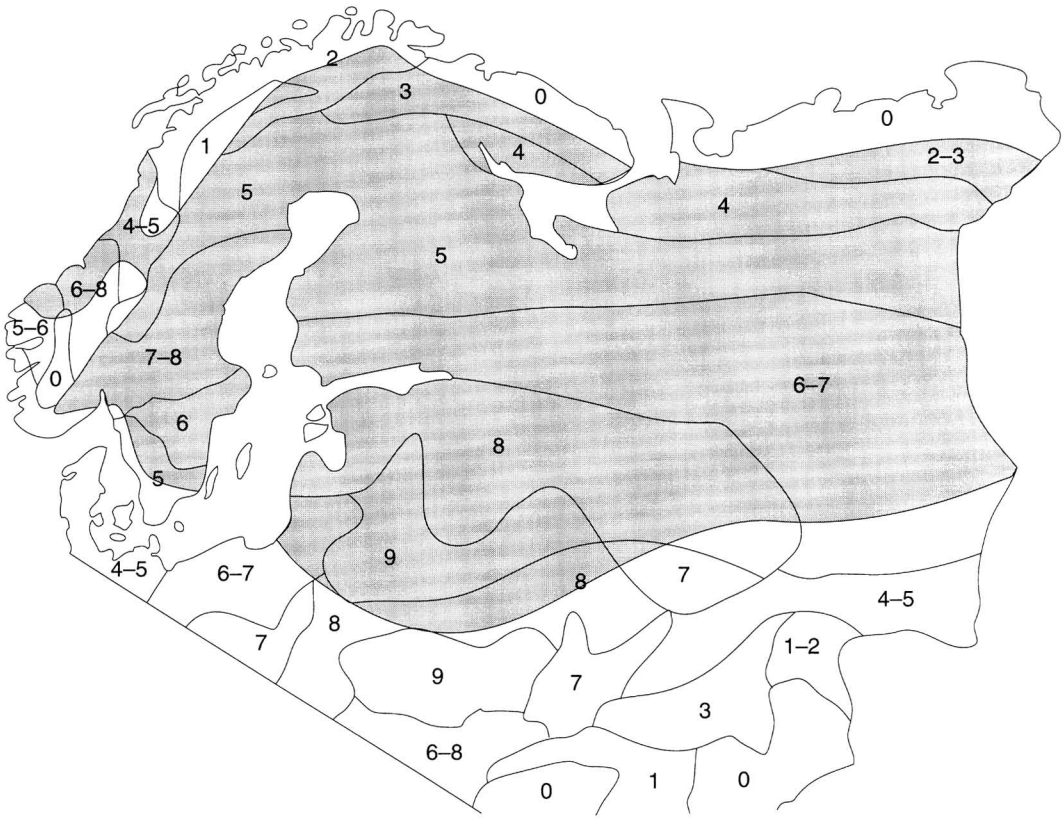

Fig. 1. Map of the distribution of boreal/hemiboreal forest as well as the number of woodpecker species in northern Europe. In the north there is tundra, in the south-east is steppe, and in the south and south-west is lowland temperate forest. Data from Cramp (1985), Ahti et al. (1968), and Mayer (1984).

landscapes (see also Angelstam in press). Since recent quantitative analyses of the effects of forest management in Swedish forests have been published, we focus on Sweden as an example. Finally, we discuss how the spatial and temporal dynamics of woodpeckers in managed boreal forest landscapes differ from those of the naturally dynamic boreal forest landscape.

2. Biogeography of woodpeckers and forests in northern Europe

In Europe there are 10 species of woodpeckers: wryneck *Jynx torquilla*, grey-headed woodpecker *Picus canus*, green woodpecker *Picus viridis*, black woodpecker, great spotted woodpecker, middle spotted woodpecker *Dendrocopos medius*, Syrian woodpecker *Dendrocopos syriacus*, white-backed woodpecker, lesser spotted, and three-toed woodpecker. The number of woodpecker species vary considerably among forested regions, ranging from 1 to 9 species (Fig. 1). Except for in mountainous areas with interdispersed patches of tundra in Norway, there are two clear gradients. From the two areas with nine species in east-central Europe (one northern with all species mentioned above except Syrian woodpecker, and one southern without three-toed woodpecker), the number of species decreases towards the north (tree-less tundra), and towards the south-east (tree-less steppe).

The northern half of Europe contains two main forest types, boreal/hemiboreal and lowland temperate forest (Ahti et al. 1968, Mayer 1984, Jahn 1991). Conifers are the main group of tree species in late successional stages of boreal forests. Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* form 100 to 98% of the conifers in the western and eastern part, respectively, of the boreal forest in Europe. In the eastern part of European Russia, Siberian pine *Pinus sibirica*, Siberian fir *Abies sibirica* and Siberian larch *Larix sibirica* form the remaining 2%. Birches, *Betula pubescens* and *B. pendula*, and aspen *Populus tremula*, dominate in early and mid-successional stages which are common in naturally dynamic boreal forests, but not in managed forests (Kuusela 1990, Shugart et al. 1992). Hence, in the boreal zone, the forest landscape is often not covered by forest in the sense that there would always be a closed canopy of large trees. The hemiboreal zone immediately south of the boreal zone ends at the southern edge of the distribution of lowland Norway spruce. Thus this zone forms a transition to the lowland temperate forest zone characterized by oaks, *Quercus petraea* and *Q. robur*, in the eastern part dealt with in this paper, and by beech *Fagus sylvatica* in the south-west. Throughout the different parts of the lowland temperate forest zone, elm *Ulmus* spp., ash *Fraxinus excelsior*, lime *Tilia cordata*, hornbeam *Carpinus betulus* and maple *Acer* spp., occur in mixed mesic stands, and black alder *Alnus glutinosa* in wet forests. Finally, in the south-east, close to the Black sea and the Volga, the temperate region grades into the steppe region (Jahn 1991).

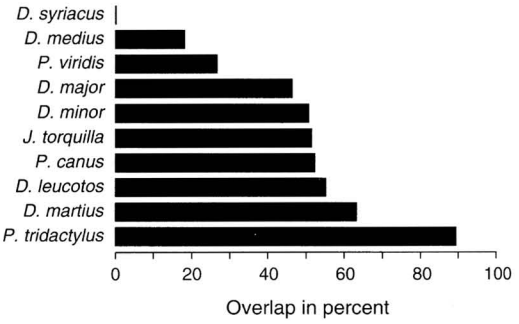

Fig. 2. The proportion of the range of the ten European woodpecker species, that overlap with boreal/hemiboreal forests. Data from Cramp (1985), Ahti et al. (1968) and Mayer (1984).

To find out to what extent the woodpecker species are found in regions with boreal/hemiboreal forests, we estimated the degree of overlap between the range of each species and the distribution of boreal/hemiboreal forest in Europe (Fig. 2). The Syrian woodpecker does not occur in boreal/hemiboreal regions, and is therefore excluded in the following presentation.

3. What is quality for woodpeckers?

The feeding and nesting site selection are summarized in Tables 1 and 2. In this section we attempt to rank the nine different woodpeckers in relation to their sensitivity to habitat changes.

Table 1. Tree species as feeding substrates for woodpeckers in boreal forest.

Woodpecker species	Sample size	Feeding substrates use in %							Source
		Aspen	Birch	Alder	Pine	Spruce	Larix	Other	
Picus canus	9	11	11	11		22	33	11	Vikberg 1982
Dryocopus martius	10	10	10		40	30		10	Vikberg 1982
Dendrocopos major	337	5	24	8	51	7	1	2	Vikberg 1982
	113		1	3	96				Hogstad 1978[a]
D. leucotos	1031	19	34	13	2	2		30	Aulén 1988
	30		46		17	37			Hogstad 1978[a]
D. minor	77		53	28		19			Hogstad 1978[a]
	11	9	45	27	9			9	Vikberg 1982
Picoides tridactylus	305	+		+		100			Hogstad 1978[a]
	20		10		40	50			Vikberg 1982

[a] winter data

During the breeding season the wryneck inhabits openings in mixed deciduous/coniferous forest, and park-like anthropogenically formed habitats (Cramp 1985, Koskimies 1989). Closed spruce forests are not used. The main food is ants, but if they are not abundant as during very hot or cold periods, other arthropods are eaten (Glutz von Blotzheim 1980). During the non-breeding season the wryneck is found in tropical steppe and savanna habitats in Africa (Salomonsen 1972).

The grey-headed woodpecker uses mixed coniferous/deciduous forests, and prefers light or open old deciduous woodlands (Koskimies 1989). In Norway the population density was positively correlated with the amount of aspen (Stenberg & Hogstad 1992). The diet of the grey-headed woodpecker is basically ants, but the species is less specialized on ants than the green woodpecker. In addition aphids, beetles and their larvae, as well as fruits and seeds are eaten (Glutz von Blotzheim 1980). Its feeding behaviour is more arboreal than that of the green woodpecker. It is mainly a resident species, but may occasionally wander to areas south and north of the main distribution range (Haftorn 1971, SOF 1990).

The green woodpecker breeds in open woodlands, or in deciduous forests but avoids large closed forest stands. It is found in forests with a higher proportion of deciduous trees than in forests preferred by the grey-headed woodpecker. The green woodpecker feeds mainly on ants throughout the year and spends more time on the ground than the other woodpecker species (Cramp 1985). The green woodpecker is a resident species (Haftorn 1971, SOF 1990).

The black woodpecker is found in most forest types and feeds almost exclusively on insects (Cramp 1985). In summer the diet of the species

Table 2. Tree species use for nesting holes by woodpeckers in boreal/hemiboreal forest. ? = proportion not indicated.

Woodpecker species	Sample size	Tree species use in %						Source
		Aspen	Birch	Alder	Pine	Spruce	Other	
Picus canus	11	91					9	Hågvar et al. 1990
	7	57	28		15			Lind 1981
	5	100						Nilsson 1942
Picus viridis	65	88	8				4	Hågvar et al. 1990
Dryocopus martius	205	32	4		26		38	Johnsson 1993[a]
	88	69			31			Johnsson 1993[b]
	102	66	2		32			Hågvar et al. 1990
	83	31	1	1	67			Östlund 1987
Dendrocopos major	324	72	5	7	11	+	5	Malchevski & Pukinski 1983
	132	29	6	28	3	2	32	Wesołowski & Tomiałojć 1986
	106	78	12	1	1	5	3	Hågvar et al.1990
	74	72	8	5	?	?	15	Aulén 1988
	46	63	11		4	11	11	Hansson 1992
D. medius	73			21		4	75	Wesołowski & Tomiałojć 1986
	39	18	28	26	3	3	22	Pettersson 1984
D. leucotos	140	45	30	22	?	?	3	Aulén 1988
	14	7	7	29			57	Wesołowski & Tomiałojć 1986
	11	36	45	9			9	Hågvar et al. 1990
D. minor	88	14	29	41			16	Nilsson & Pettersson 1990
	50	40	34	26				Hågvar et al. 1990
	19			47			53	Wesołowski & Tomiałojć 1986
Picoides tridactylus	19	11		16	5	68		Wesołowski & Tomiałojć 1986
	13	31				69		Hågvar et al. 1990
Jynx torquilla	27	22	44	22	4		8	Linkola 1978

[a] data from Småland (south Sweden)
[b] data from Uppland (central Sweden)

is based mainly on ants, but in winter the species eats also beetle larvae (Pynnönen 1939, 1943). Occasionally the black woodpecker eats berries and fruits. The black woodpecker is mainly resident, but in September and October migration movements may occur (SOF 1990).

The great spotted woodpecker may occur in any wooded habitat. It may even be found in agricultural landscapes with tree rows only (O'Connor & Shrub 1986). The species also the most omnivorous species (Cramp 1985). In summer it feeds on beetles and beetle larvae in dead wood, aphids in the canopy of deciduous trees, and on ants. In autumn berries are eaten, and in winter the diet consists mainly of Scots pine and Norway spruce seeds. Probably following the seed set of pine and spruce, it invades new ranges (such as in 1929, 1935, 1962, 1988 (Salomonsen 1972, SOF 1990)). Some invasions reach even central Europe, the British Isles (Haftorn 1971) and the Faeroes (in 1929 and 1935 — Salomonsen 1972).

The middle spotted woodpecker inhabits broad-leaved deciduous and mixed forests in central Europe (Cramp 1985). In Sweden it was dependent on old, open, oak-dominated forest (Pettersson 1984). This very specialized, resident species feeds almost entirely on insects.

The white-backed woodpecker is found in deciduous and mixed forest, now often along shores and field edges (Aulén 1988, Koskimies 1989). While foraging it may fly several kilometers along such linear habitats; it was favoured by slash-and-burn cultivation (Koskimies 1989). In Norway it may also occur in coniferous stands if enough rotten wood is present as the diet consists mostly of insects (larvae of beetles) obtained from dead trees (Håland & Toft 1983). It is mainly resident but invasion-like migrations may occur (SOF 1990, Tiainen 1990).

The lesser spotted woodpecker prefers old unmanaged, deciduous forests (Svensson et al. 1992), and it feeds exclusively on insects. In summer it feeds on aphids in deciduous trees, ants, beetles and even flying insects. In the autumn it starts feeding on insects found in dead wood and in bark crevices. Sun-exposed trees provide more food (Nilsson et al. 1992) suggesting that closed canopy forest is less suitable for the lesser spotted woodpecker. It is mainly a resident, but with slight invasion tendencies (SOF 1990).

The three-toed woodpecker prefers old spruce forests, but may accept old pine forests as well as birch forest in the north (Koskimies 1989). It may persist for long time in climax spruce forest (Haapanen 1965) and is the only species using mainly spruce trees for nest hole excavation (see also Table 2). The three-toed woodpecker successfully colonizes clear-cuts if dead standing trees are left, or if edges contain damaged or dead trees (Ahlén 1975a, Anufriev pers. comm.), as well as areas with storm damaged forest (Virkkala et al. 1991). Throughout its range, the distribution of the three-toed woodpecker is closely tied to *Picea* spp. (Bock & Bock 1974), and it immigrates to new areas of spruce growth (Ruge & Weber 1974). The three-toed woodpecker feeds mostly on wood-boring beetles, and sometimes is "ringing" trees for sap. In Colorado the abundance was correlated with the abundance of spruce bark beetle abundance areas (Massey & Wygant 1973). It is mainly a resident species, but movements occur yearly, and in some years it invades areas outside the normal breeding range; such as 1974–75 in southernmost Sweden (SOF 1990, Cherrug et al. 1990).

In summary, we group the nine boreal/hemiboreal woodpecker species in relation to the sensitivity to changes in forest structure and composition as follows:

1) Great spotted woodpecker. Feeds mainly on abundant conifer seeds and has a good dispersal ability.
2) Black woodpecker. Feeds on ants in wood and on the ground as well as on insects in many types of dead wood (including stumps left after logging). It can inhabit pure coniferous as well as pure deciduous forest, but requires large trees for nesting hole excavation.
3) Wryneck, and green woodpecker. Feed on ants on the ground, but require deciduous forest (ranked according to the increasing demands of deciduous forest). This group of species seems to be also dependent on old-fashioned agricultural activity. The wryneck is migratory and does not excavate own nest holes.
4) Grey-headed woodpecker. Is similar to the two previous species but feeds also on insects in dead wood.

5) Three-toed woodpecker. Feeds on invertebrates in coniferous wood.
6) Lesser-spotted, white-backed, middle-spotted woodpecker. Feed mainly on deciduous dead wood (ranked according to sufficient diameter of trees for nesting, and to increasing rarity of tree species hosting important food items).

4. Landscape components in the pristine boreal/hemiboreal forest

A clear starting point for analyses of why the woodpeckers as a group have declined (see Table 3), is to describe how much the different natural properties of forest have been changed by forest management, and try to estimate the structures of the landscape where woodpeckers originally occurred or evolved.

The diversity of biotopes in any natural landscape is set on the one hand by the differences in soil types, topography, access to nutrients and water, and by disturbance regimes on the other. Disturbance regimes vary along continuums from large-scale (fire, hurricanes, insect outbreaks) (Hunter 1990) to small-scale (gap regeneration) (Falinski 1986, Jahn 1991, Frelich & Lorimer 1991), and from frequent to infrequent.

The dominating, frequent, and large scale disturbance factor of the natural boreal landscape was fire (Kohh 1975, Zackrisson 1977a, 1977b, Engelmark 1984, 1987, Granström 1991, Zackrisson & Östlund 1991). On average, in a large region, 0.5–2% of the landscape is affected by forest fires annually (Bonan & Shugart 1989). The variation around these means is, however, very large and the important fire periods creating the major landscape patterns may be several decades apart (Romme & Despain 1989). In addition, few and large burns affect the landscape the most (Hunter 1990). However, even within large forest fires, many patches with surviving trees remain in large burned areas (Johnson 1992), and such fire refugia occur in a partly predictable way according to moisture and topography (Zackrisson 1977b, Engelmark 1987; review in Angelstam et al. 1993; see also Fig. 3). Also in hemiboreal zone, forest fires are common on dry sites and there is a negative correlation between fire frequency and soil moisture (based on data in Kairiukstis 1968).

5. How has forest management changed structures?

The dynamics of managed forest differs from that of the natural forest in several ways, both structurally within a stand and with different disturbance frequencies within the whole landscape (Harris 1984, Hunter 1990, Angelstam et al. 1990, Esseen et al. 1992, Angelstam 1991, 1992, Johnson 1992). Even if large clear-cuts sometimes superficially mimic the large-scale character of burns, it is important to note that burned areas have an enormous structural diversity compared with traditional clear-cuts. For example, usually less than 10% of the wood is

Table 3. Woodpecker species ranked according to degree of specialization in relation to recent population trends, population size and status in Red Data Book in Sweden (Ulfstrand & Högstedt 1976, Ahlén & Tjernberg 1992, Nilsson et al. 1992).

Species	Population trend	Population size (pairs)	Status
Dendtrocopos major	no	200000	
Dryocopus martius	decrease in N	20000–30000	vulnerable in N
Jynx torquilla	decrease	20000	
Picus viridis	decrease	50000	
P. canus	decrease	100–200	rare
Picoides tridactylus	decrease	5000–15000	vulnerable in S
Dendrocopos minor	fast decrease	5000	vulnerable
D. leucotos	fast decrease	60	endangered
D. medius	extinct 1982	0	extinct

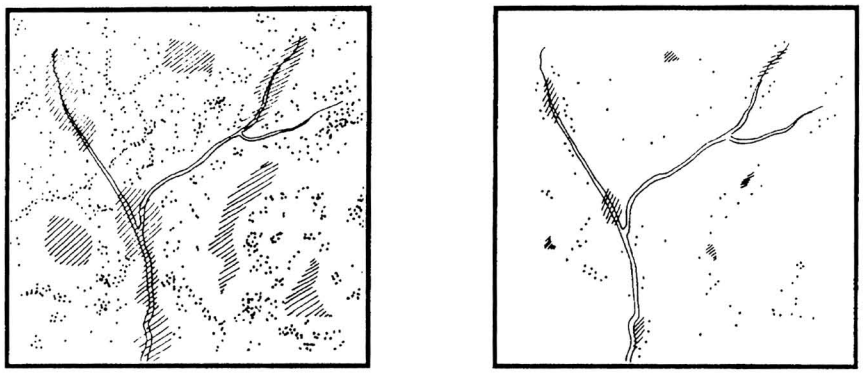

Fig. 3. Principal differences between the distribution of deciduous forest in a naturally dynamic (left) and a managed (right) landscape. In the natural landscape the deciduous component is found as single trees or groups of trees (dots), as transient successional stages (hatched areas), and as a stable network in wet forests along water (lines).

consumed during a fire, leaving large volumes of standing and downed wood (Foster 1983, Payette et al. 1989), while 95–98% of the wood is removed after clear-cutting in Sweden (Hultkranz & Wibe 1989). Below we describe some major changes in forest landscapes which should have affected woodpeckers.

In spite of a long history of logging, the amount of forests older than about 100 years has not changed very much during the 20th century (Mattson & Stridsberg 1981, Kempe et al. 1992). However, several properties of the forest stands have changed.

Between 1886 and 1991 in the middle taiga forests at the 62nd parallel, trees larger than 34 cm of the diameter at breast height (DBH) declined from 44 to 7 trees per ha and trees larger than 42 cm DBH declined from 14 to one per ha (Linder & Östlund 1992). These changes have occurred gradually and are typical for all of central and northern Sweden.

In 1887–1930 in central Sweden about 20% of the standing biomass in forest was made up of dead trees (Nilsson 1933). Linder & Östlund (1992) found that in two areas in the middle taiga of Sweden, the amount of dead standing trees per ha had decreased gradually from 13 in the 1890's to 0.1 in 1966. Kohh (1975) reports similar changes from a nearby area.

For fallen dead wood there is no official statistics. Linder (1986) found about 70 cubic meters per ha in mountain spruce forests dominated by internal stand dynamics. Such stands once covered fairly large proportions of the landscape. In northern Sweden, Zackrisson & Östlund (1991) reported that such spruce forests comprised between 25 and 30% of all forests. Comparisons of forest structure in managed Swedish and in natural Russian pine forest show that the amount of dead standing trees is 33 times higher, dead laying trees 46 times higher and large trees 8 times higher in the latter than in the former (Angelstam et al. unpubl.). Today the proportion of dead trees in the forest is less than 2% of the stock (Kempe et al. 1992).

Most woodpeckers prefer large trees and deciduous tree species for excavating nest holes (Table 2). The deciduous tree component consists of three types (Fig. 3). First, the deciduous trees that are found within conifer-dominated stands in naturally dynamic forests; secondly the deciduous forest that forms transient successional stages occurring some time following fire; and third the deciduous admixture found in more or less permanent corridors along unregulated rivers.

The amount of deciduous trees has remained roughly stable during the period when forests have been surveyed, and the amount of large deciduous trees has even increased (SOU 1992). The occurrence of adult deciduous trees is now largely confined to the edge between boreal forest and abandoned farmland (Ihse et al. unpubl.).

In the conifer-dominated parts of the boreal landscape there has been a reduction in the amount of deciduous trees (Gjerde et al. 1992). However, this decline started before the forest survey started (cf. Zackrisson & Östlund 1991).

For the second successional deciduous tree component there are no official statistics. In historical reconstructions of the pristine landscape the proportion of successional stands with a high proportion of deciduous trees was 8% in one study in central Lapland (Zackrisson & Östlund 1991).

The changes in the amounts of permanent more or less linear stands is difficult to assess, but most rivers are either regulated or the fertile soils have been turned into agricultural land so the reduction in this kind of forest must be very large.

Obviously this must have affected species demanding dead wood and old deciduous trees.

Indirect effects of landscape changes

The human use of forests has also influenced processes that cover the whole landscape. For example altered densities of large predators has effected herbivores feeding on deciduous trees which then influence the browsing pressure, thereby altering future tree species composition (Alverson et al. 1988, Pastor et al. 1988). The dominating browser in taiga forests is the moose (*Alces alces*). In Sweden the moose has increased dramatically during the last 50 years due to low natural mortality and increased amounts of young forest providing a good food supply (Strandgaard 1982). Moose prefer deciduous trees over conifers as winter food (Ahlén 1975b). Intensive browsing may thus prevent deciduous tree species from growing into an adult shape and reproducing. This is a serious long-term conservation problem for hole-nesters (see Table 2). In addition to forest management, this indirect effect of browsing reduces the future occurrence of the previously common old decidous trees in taiga forests.

Another important altered process is the disappearance of the effects of megaherbivores (Andersson & Appelqvist 1990) on vegetation in past hemiboreal/temperate forests. After the extinction of the big herbivores (mammoth, wood elephant, rhinoceros, European bison, aurox) at the end of the Weichselian (Kurtén 1964, Nilsson 1972), the role of man in keeping the landscape open increased. This applies first of all to the broad-leaved deciduous forest, but also to the hemiboreal zone. Elements of the parklike woods of the Pleistocene, like old trees and open grazed woods, thus survived in ancient agriculture. In temperate forests this important habitat is disappearing as pure forestry takes over and when old-fashioned agricultural methods producing open forest with grazed ground are abandoned (Andersson & Appelqvist 1990). This scenario would have affected species like the green woodpecker and the wryneck.

6. Forest history and woodpeckers

Even if there have been only slight changes in the amount of forest land and old forest, from a forestry point-of-view, a number of properties that are critical for woodpeckers have been severely reduced. Consequently, woodpecker species are responding accordingly (Table 3).

The number of the most generalistic species, the great spotted woodpecker, is fluctuating. In Belgium, the Netherlands, Denmark and Fennoscandia, the species has increased and expanded during the present century owing to increased afforestations, and possibly also to climatic changes (Cramp 1985). In Northern Europe it fluctuates largely with the variation in food supply. Nilsson et al. (1992) found an effect of spruce seed abundance on the size and rate of change of great spotted woodpecker population in Sweden. Nevertheless, the species is more common in unmanaged than in managed forest (Nilsson 1979, Angelstam 1990, Scherzinger 1990). Rutschke (1983) found that densities in pine woods were only 10–20% of those in broad-leaved woodlands.

The black woodpecker has been considered as declining species in Finland (Järvinen et al. 1977 but see Majewski & Rolstad in press), and also in northern Sweden (Ahlén & Tjernberg 1992), but in several European countries it is increasing as a consequence of increasing forest cover (Cuisin 1985). In southern Sweden there is no overall population trend, but a positive association between mild winters and abundance in the next year exists (Nilsson et al. 1992).

The numbers of wrynecks have decreased strongly during the 1980's in Sweden (SOF 1990).

Termination of cattle grazing is harmful for the species (Linkola 1978). Reduced grazing pressure leads to reduced amount of patches with short, dense turf, which is an important condition for diverse ant populations (Marchant et al. 1990).

The grey-headed woodpecker is one of the least known breeding birds in Sweden, and from 1961 to 1975 there were only six recorded breeding attempts (SOF 1990). It may have increased in southern Sweden but has a very low populations size: 100–200 pairs in the whole of Sweden (Ahlén & Tjernberg 1992). The trend of the species is considered negative.

The green woodpecker is restricted to the hemiboreal zone and is declining slightly in Sweden, probably due to continuous disappearance of suitable habitats (pastures with scattered trees) (Nilsson et al. 1992). Observations reviewed by Ekman (1922) suggest that the green woodpecker had a much more northerly distribution during the late 19th century, when pastures were more common. Population changes in the UK are probably related to declines in sheep husbandry and in rabbit populations which reduces the amount of ant populations (Marchant et al. 1990; see also wryneck).

The three-toed woodpecker has declined sharply outside its core area in mountain forests in northwestern Sweden (SOF 1990, Svensson et al. 1992). Virkkala (1987) found that three-toed woodpeckers were less common where old forests were fragmented. However, its opportunistic use of habitats and invasion tendencies seem to allow rapid recolonization once resources become available. Accordingly, after severe storms in Sweden and Norway in the late 1960's (Svensson et al. 1992), as well as in an area with storm disturbance in Finland (Virkkala et al. 1991) it increased temporarily as dead wood became available. Creation of new beaver ponds may also produce suitable patches of habitat (see Lochmiller 1979).

Since the middle of the 1970's the lesser spotted woodpecker has declined with an annual rate of 7% in Sweden (Nilsson et al. 1992). Also in Finland this species has declined sharply (Tiainen 1985, Väisänen & Koskimies 1989). The lesser spotted woodpecker demands 15–25 ha of unmanaged deciduous forest (Wiktander et al. 1992). The amount of broad-leaved deciduous forest has declined by an average of 1% per year since 1960 (SNV 1982). The lesser spotted woodpecker requires smaller areas of forest, and smaller dimensions of trees than other woodpecker species. Therefore, riparian and wet forests are still sufficiently abundant to maintain local populations. The trend is nevertheless negative.

In Sweden, the white-backed woodpecker has disappeared from most boreal forests (compare Ekman 1922 with SOF 1978). In the 19th century it bred in eastern Sweden from the far south to the far north, i.e. in the areas with the highest fire frequencies (cf. Granström 1991). It first disappeared from the south and the Island of Gotland, and during the 1950's it disappeared from the north taiga forests. In 1988 the Swedish population was estimated to 80–110 breeding pairs divided in three local populations (SOF 1990). The main decline of the most specialized woodpecker species in the boreal forest probably had already started during the preindustrial period of forestry, and the white-backed woodpecker became extinct from most of the boreal forest shortly afterwards (Ekman 1922, SOF 1978, Aulén 1986). After a severe decline 20–30 years ago it became endangered (Aulén 1988). The development in Finland has been similar with a drastic decline to 30–40 breeding pairs at present (Virkkala 1988, Tiainen 1990, Virkkala et al. 1993). In eastern Norway the forests, near nests, contained an average of 44% birch and aspen, and 8% dead wood (Gjerde et al 1992). Since forest fire no longer occurs as a dynamic factor in Swedish forests, the successional habitats are not being created any longer in the forest landscape. The white-backed woodpecker is thus about to go extinct from the boreal forest, and the species is still present in Sweden only because suitable habitats, with deciduous forest under free development, have been created on farmland that was abandoned 30 to 50 years ago (Aulén 1988, Nilsson & Pettersson 1990, Angelstam et al. 1993). In western Norway the white-backed woodpecker is still common (700–900 pairs) (Håland & Ugelvik 1990). This is probably due to the complicated and steep topography which makes forest management difficult or impossible. Mild winters, heavy rainfalls and high humidity probably speed up decay of wood. Steep slopes protect against exploitation of forests, and ava-

lanches break trees frequently (Håland & Ugelvik 1990, Stenberg 1990, Stenberg & Hogstad 1992). In some areas in Norway it is the most common woodpecker species (Stenberg 1990, Stenberg & Hogstad 1992). Furthermore, it still thrives in Latvia (Viksnes 1989), in Estonia (Renno 1993) and the eastern part of Poland (Tomiałojć 1990).

During the mid 19th century the middle spotted woodpecker was found breeding in mixed forest and farmland landscapes with large deciduous trees, primarily oak, in southernmost and south-central Sweden. The last observed breeding pair in the southern population was recorded in 1948, and the population in south-central Sweden went extinct in 1982 (Holmbring & Pettersson 1983, Pettersson 1984), and in Denmark it became extinct in 1961 (Salomonsen 1972). Since then the species has been recorded only once, on the Falsterbo peninsula in southwesternmost Sweden (Cherrug et al. 1989).

In conclusion, apparently some woodpecker species declined, from the human pre-settlement period dominated by large burned areas interspersed with large unburned areas, to the early 20th century, with large continuous tracts of selectively cut forest. The comparison between the degree of specialization, the changes in forests and recent population trends shows a good fit (Table 3).

7. Dynamics of woodpeckers in natural boreal/hemiboreal forests

What were the spatial and temporal dynamics of the woodpeckers in the naturally dynamic forest? In the following discussion we concentrate on the woodpeckers that occur mainly in hemiboreal and boreal forests (Fig. 2), since the knowledge about the dynamics in the natural undisturbed forest landscape is best known for this forest vegetation zone.

We propose that in a naturally dynamic boreal/hemiboreal landscape the occurrence of the different woodpecker species probably were linked to different disturbance regimes (Fig. 4).

The white-backed, lesser spotted and the grey-headed woodpeckers were adapted to the late stages of the deciduous phase in the succession after forest fire, and to permanent corridors of forests with a high proportion of deciduous trees along water.

The three-toed woodpecker was probably found mainly in forests with internal dynamics, but expanded to windblown forest or late successional after fire as such habitats became available. Todays' apparent confinement to old spruce forest (eg. Cramp 1985) may thus be an artifact as post-fire successional stages with high proportions of dead deciduous and coniferous wood are lacking. Russian observations suggest that the three-toed woodpeckers occupy large burns, as well as the old spruce forest (Teplov unpubl.). Analogously, Wesołowski & Tomiałojć (1986) found that three-toed woodpecker preferred swampy ash-alder stands before coniferous stands.

The black and the great-spotted woodpecker were ubiquitous but became probably even more abundant when the suitable structures became more abundant such as after fire and wind.

Based on the spatial dynamics it is possible to hypothesize about the temporal dynamics of the different species. The dynamics of the great spotted woodpecker follow the seed set of conifers, but probably also responds to increases in the amount of deciduous dead wood in successional stages following fire. The lesser spotted, white-backed, and the grey-headed woodpeckers have a minimum average density related to the amount of riparian forests, and these species expand into deciduous dead wood in successional stages following fire. Finally, the three-toed woodpecker also has a minimum average density related to the amount of riparian and mountain forests, and it expands into the fire-dominated landscape shortly after fire, during the late successional phase, and into any habitat during insect outbreaks after storm fellings (Virkkala et al. 1991). The density of the black woodpecker was probably stable, alternating between dead wood found in old forest and dead wood found after storm fellings and forest fires.

8. Management implications and further research

This review clearly shows that maintenance of habitats demanded by woodpecker species as a

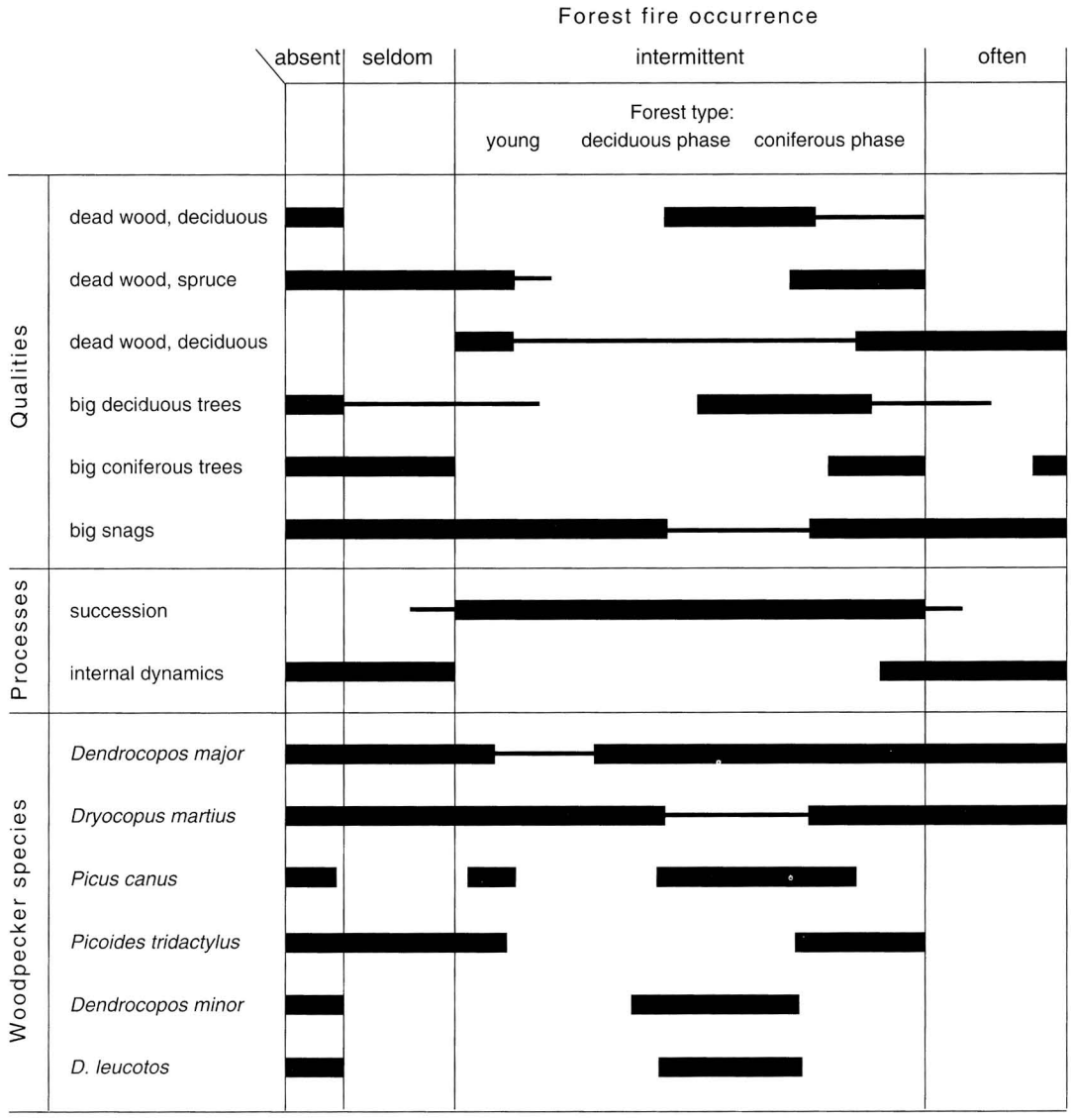

Fig. 4. The distribution of different important properties in a gradient from wet forests undisturbed by fire, to dry forests frequently disturbed by fire, and the distribution of different boreal and hemiboreal woodpecker species. Four major types of fire frequences are recognized (for details see Angelstam et al. 1993 and Angelstam in press) viz.; 1. Fire is absent and internal dynamics prevails on wet sites. Wet soils are usually situated near water, and therefore fire refugia often form an important linear landscape component along the edge between water and land. Wood in different stages of decay is continuously present even within a small area. 2. Fire occurs seldom on moist sites. Such forests are complexes of two disturbance regimes, namely fire under extreme droughts, followed by long periods with internal dynamics. This produces forest stands that are dominated by a continuous and uneven-aged tree cover and often also a continuous supply of dead wood in different stages of decay. 3. Fire frequencies are intermediate (70–100 years (Zackrisson 1977a, 1977b, Bratt et al. 1993) on mesic sites. Fires on mesic sites are followed by a well developed phase with successional trees. On some sites the deciduous phase may be kept almost permanent by intermittent fires. 4. Fire occurs often (every 30–50 years (Kohh 1975, Zackrisson 1977 a, 1977b, Engelmark 1984, 1987)) on dry sites. In dry taiga forests west of the Ural mountains, Scots pine is the dominating tree species. Natural forests on dry sites are characterized by complex structure and poorly developed or no deciduous phase. The proportions of the different site types is proportionate to the occurrence of these site types in Sweden (Angelstam et al 1993).

group are in conflict with intensive forest management. If we want to keep viable populations of all woodpecker species in a landscape, the forest stands and landscapes have to be actively managed to increase the number of old, dead and deciduous trees. This involves both preservation of the existing valuable forests, but also active reconstruction of the reduced habitat types by speeding up the production of dead wood (Gjerde et al. 1992), as well as reduction of browsing pressure. For the typical ant-eating species like wryneck, green woodpecker, and to some extent for the grey-headed woodpecker, the maintenance of some open wooded habitats in the landscape is necessary.

To find out the amount of different important structures and forest types required for maintaining viable populations of the different woodpecker species, it is nessesary to find large reference areas representing a gradient from natural to managed forest landscapes. The future should include studies of distribution, abundance, habitat niche breadth and fitness of different woodpecker species in landscapes with different arrangements of habitats, representing stable networks of wet or mountain forests as well as transient successional stages. Several woodpecker species would thus also be suitable for setting up quantitative goals for forestry, and woodpeckers could be used as monitoring tools and indicators of successful habitat restoration.

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