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Preserving ecological diversity in boreal forests: ecological background, research, and management

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Constrasting views are held about the possibility of developing ecologically sustainable forestry in northern boreal forests, the taiga. Foresters tend to be optimistic, but they evaluate 'sustainability' on the sole basis of timber production, whereas some environmentalists express very pessimistic views. The conflict can be resolved on substantial arguments, backed by ecological data. I review ecological characteristics of the taiga and the consequences of modern forest management for the forest fauna, particularly in northwestern Europe. Uniform 'monoculture' would be disastrous for a majority of forest species, but it is, fortunately, impossible to attain: heterogeneity in forest vegetation and stand structure remains. This improves prospects of maintaining a diverse fauna in appropriately managed forests. Systematic surveys to detect patterns in abundance variation, and assessments of ecological conditions for population viability ('minimum requirements') of target species are urgent research priorities. The taiga seems to be a resilient ecological system, and the possibilities of modifying management practices such that they match forest dynamics seem good. I discuss recommendations drawing upon conclusions presented in other papers in this issue.

1. Introduction: contrasting views of the taiga

The boreal coniferous forest, the taiga, is one of the most extensive biomes on the earth. It extends as a broad belt over both the Palearctic and the Neartic. Boreal forests have been under human influence for thousands of years, and commercial forestry reached parts of the zone at least two centuries ago. The model of modern intensive silviculture that was later to be applied all over the boreal zone originated in the coniferous forests of central Europe, particularly in Germany, as a response to a threatening timber shortage in the 18th century (Radkau 1983). Cuttings were started in an extensive 'mining' fashion without paying attention to forest regeneration, and forestry science grew out of the timber shortage shock that necessarily followed (Radkau & Schäfer 1987).

There have been shifts in the ways forests are perceived by forestry science, which vary from country to country depending on cultural relationships to forests and idiosynchracies of research traditions, but a review of this development is beyond the scope of this essay. The dominating paradigm which became widely adopted during the 20th century was monoculture, based on the assumption that timber growth is maximized in even-aged, single species stands brought forth by clear-cutting, soil preparation, artificial fertilization and planting with carefully selected and bred plant material. The aim was to create uniform conditions for tree growth on the scale of forest stands, unit stand size being several tens of hectares. The ultimate shift to monoculture forestry occurred for instance in Finland in the early 1950s and, as a consequence, previous botanically and ecologically oriented research traditions were marginalized within forest research institutions.

The aim of modern forestry has been, ever since its conception, to develop methods that allow 'sustainable forest use', but with timber production as the sole criterion of sustainability. In the short run, monoculture seems to fullfil this aim in boreal forests, but this is deceptive. Monoculture has been subjected to increasing criticism on silvicultural and economic grounds. Monoculture is expensive, harmful in the long term to the productivity of forest soils, and often impracticable as maintaining stand uniformity needs constant attention: heterogeneity is rapidly restored because of variation in, for instance, soils, drainage and microclimate. There is an increasing awareness that the productivity of boreal forests is maintained by processes that are heterogeneous in space and time. A view emphasizing 'dynamic landscape heterogeneity', that is, mosaic-like distribution of different stand types, shifting in time, is more appropriate than the homogeneous stand ideal (Mladenoff & Pastor 1993).

Furthermore, sustainable timber production does not equal ecological sustainability. A major criterion of ecological sustainability is that the original suite of species remains viable. However, as conservationists have pointed out for decades, the creation of forest monocultures brings about an impoverishment of the forest fauna and an increasing risk of extinction of specialized species (Rassi & Väisänen 1987, and other Red Data Book reports from countries in the boreal zone).

Large areas of the taiga are still untouched by intensive forestry, but the pressure is rapidly growing, particularly in the former USSR as a consequence of economic transformations following the collapse of the old rule. This creates a burning need for recommendations about how forestry practices adopted under the monoculture paradigm should be modified.

Some environmentalists are utterly pessimistic about the chances of developing sustainable forestry in the taiga. 'Taiga news', an international newsletter for environmental action groups, recently carried the following in an editorial (no. 6, 1993): 'BOREAL TIMBER HAS MANY TIMES been put forward as a more "sustainable alternative" compared to tropical timber. Today we know that there is no such thing as sustainable commercial forestry anywhere in the world, at least not on a national level'.

This pessimistic view is supported by experience from the mechanistic application of the monoculture paradigm, and also by various social experiences such as the frustrations stemming from conflicts with forest administrators over the logging of remaining old-growth forests. In the background there is also a metaphysical belief in a basic disharmony between human activities and a presumed 'balance of nature'.

Thus, this pessimism is open to question in the same way as is the unproblematic faith in monoculture voiced by foresters in past decades. The authors of the 'Taiga news' editorial take it for granted that forestry is in contradiction with forest ecology, but this is by no means self-evident. Natural disturbances are an integral part of the ecology of boreal forests, and there are no a priori reasons why human induced disturbances could not be incorporated into or based upon natural disturbance dynamics. Data based evaluations of the ecological characteristics of boreal forests and the effects of alternative management practices on forest organisms are needed.

In this essay I dicuss relationships between forestry and the taiga. I do not repeat arguments presented in other papers in this issue of Annales Zoologici Fennici. My purpose is, instead, to raise questions on a more general level and suggest topics for further work. I start by discussing ecological characteristics of the taiga with the purpose of identifying those features that are important for assessing the consequences of human modification. Then I review available data on the effects of modern forestry on forest fauna, particularly the results of studies conducted in Finland, and make suggestions for research priorities and management.

2. The taiga: biogeographic background

The taiga is controlled by climatic conditions: it lies between the northern summer limit of the temperate airmasses and the southern winter limit of the arctic airmasses, i.e., the zone with warm summers and (very) cold winters (Delcourt & Delcourt 1991). These conditions are the product of the Ice Age and have dominated northern parts of the northern continents for the last several million years (West 1977, Imbrie & Imbrie 1979, Bartlein 1988, Heusser & King 1988, Spicer & Chapman 1990). The basic characteristics of taiga habitats are determined by plants that endure cold winters: typically species of woody plants and field and ground layer vegetation that survives the winter under the protection of snow cover (Tuhkanen 1984, Bonan & Shugart 1989, Solomon 1992). The taiga can be divided into latitudinal subzones which are distinct in the inner parts of both continents but grade into altitudinal zones close to mountain ranges (Chernov 1975, Hämet-Ahti 1981, Tuhkanen 1984, Delcourt & Delcourt 1991).

The distributional history of taiga vegetation has been extremely dynamic, particularly in areas that have been covered several times by continental ice. There is growing evidence that the composition of plant associations of the taiga is contingent upon historical accidents — the dominant tree species, for instance, have varied from one interglacial to another, and many species have gone extinct during the Pleistocene fluctuations, particularly from the western Palearctic (Birks 1986, Barnosky 1987, Watts 1988, Delcourt & Delcourt 1991). On the other hand, the extant vegetation formations tend to be strongly influenced by a few dominant plant species (trees, dwarf shrubs, mosses), and the taiga is structurally relatively uniform throughout the zone (Hare 1954, Hustich 1974, Hämet-Ahti 1981, Tuhkanen 1984).

Some elements of the fauna inhabiting boreal forests have presumably evolved in connection with the dominating plant associations. Stegman (1938) originally raised this suggestion on the basis of distribution patterns of birds, calling the taiga fauna 'Siberian faunal element'. According to Brunov (1978, 1980), this suggestion agrees with current more comprehensive data on bird distributions particularly as regards northern and central taiga, whereas in the southern subzone the proportion of species that originated in forests further south is considerable. There is paleontological evidence from small mammals (Makaev 1987) and distributional evidence from several groups of insects (Chernov 1975) that Stegman's suggestion may be valid. However, a large proportion of the animals inhabiting the present taiga are immigrants in an evolutionary sense from other biogeographic zones. The boreal zone also includes habitats such as wetlands, bogs and meadows that are inhabited by specialized species with wide geographic distributions, dubbed 'interzonal species' by Chernov (1975, 1985).

Stegman's idea of identifying a faunal element particularly adapted to the taiga might also prove fruitful in practice. As has several times been suggested, the group of typical taiga birds is potentially useful as an indicator group for monitoring faunal change (Järvinen & Väisänen 1979, Haila 1985, Virkkala 1989).

Another important although less adequately documented biogeographic feature of the taiga zone is 'longitudinal', east–west differentiation of the extant assemblages. Differences in history have probably played a large role in creating such differentiation. The Palearctic and Neartic continents differ in species identities among dominant trees and field layer plants which often belong to the same genera ('vicariant species', Hustich 1974, Nikolov & Helmisaari 1992). This is also true of carabid beetles (Niemelä et al. 1994), whereas among birds taxonomic differences are larger possibly because birds are historically constrained by their migration habits (Mayr 1946, Haila & Järvinen 1990). There seem to be differences in bird assemblage characteristics between the continents, for instance, tropical migrants seem to respond to variation in habitat structure in a more deterministic fashion in the Nearctic than in the Palearctic, and this difference is amenable to an historical explanation (Mönkkönen & Helle 1989, Mönkkönen 1994, Mönkkönen & Welsh 1994). Other examples of intercontinental community differences, often anecdotally mentioned but not investigated systematically, include shrews, red wood ants and earthworms, all more abundant in the Palearctic than in the Nearctic, and the thickness of the undergrowth in the Nearctic compared with the Palearctic. There is an intriguing imbalance in the number of herbivorous insects that have successfully colonized the Nearctic from the Palearctic compared with the much lower number of colonists in the opposite direction (Niemelä & Mattson 1992).

Another important feature of 'longitudinal' differentiation is species turnover and pronounced abundance variation across the continents. The eastern and western parts of both continents differ greatly from each other in floristic and faunistic composition. In North America, the important shift is at the Rockies (Keast 1990), and in the Palearctic along the river Jenissej (Matjushkin 1982). Such differences, variably reflected in biogeographic zonations, have their background in history on the geological/ evolutionary scale. In addition, there is important variation in forest characteristics on the regional scale that is due to, for instance, glacial history, climatic gradients such as variable degrees of continentality, variation in soil conditions, and geographically determined differences in immigration and speciation patterns (Brubaker 1975, Velicho et al. 1984, Heusser & King 1988, Watts 1988, Delcourt & Delcourt 1991, Syrjänen et al. 1994). This all implies that comparisons between different parts of the taiga are misleading without due consideration of regional-scale biogeographic variation.

Also variation in the intensity of human modification needs to be acknowledged in a 'longitudinal' survey of the taiga. Human influence extends several thousand years back everywhere in the boreal zone, but not uniformly. For instance, in northern Russia extensive human influence began only two or three centuries ago (Dolukhanov & Khotinskiy 1984), whereas in northwestern Europe intensive forest clearing for swidden agriculture and extraction of timber reached boreal forests several centuries earlier (Åström 1977). In North America, the shift from native to European methods of natural resource use has been very consequential, but it occurred in New England several centuries earlier than in north-central parts of the continent.

3. The taiga: natural disturbance dynamics

Extant assemblages of the taiga have been shaped by disturbances that change conditions locally, with a characteristic average frequency, and trigger succession in vegetation; the evidence is summarized in Delcourt & Delcourt (1991) and Shugart et al. (1992). Consequently, a landscape framework is necessary for analyzing ecological processes in taiga environments (Hansson 1992a).

Fire is commonly regarded as the most important disturbance on the scale of forest stands (the evidence is summarized in, for instance, Wein & MacLean 1983), although the role of windfalls and other, more local disturbances is probably underestimated because of their lower frequencies and less regular occurrence (Wein & El-Bayoumi 1983). There is fairly good evidence from several areas in North America that the 'shifting mosaic steady state' model (Loucks 1970, Shugart 1984) may be adequate for describing variations observed in local pollen records of dominant trees (summarized in Delcourt & Delcourt 1991). On the scale of patch dynamics, the taiga apparently has been in a steady state for some thousand years in some parts of the zone. However, in some other parts tree species distributions and dominance relationships have changed more or less continuously, presumably tracking long-term climatic fluctuations, in an essentially non-equilibrial fashion on the short term. Examples include the invasion of spruce and tree-limit changes in the Scandinavian mountains (Kullman 1991, Kullman & Engelmark 1991) and changes in tree age and stand composition in Yellowstone Park and the Pacific North West (Sprugel 1991). Such evidence for continuous, non-equilibrial natural change has implications for conservation: there is no clear-cut 'natural standard' to be found in the past for using as a model for the future.

Wildfires seem to form an appropriate background for understanding cyclic changes in local animal assemblages (Heinselman 1981, Fox 1983, Esseen et al. 1992, Haila et al. 1994), but in elaborating this conclusion one comes across the following difficulties that have not been systematically addressed (Payette 1992, Syrjänen et al. 1994):

(1) The severity of an 'average' fire is an open issue. The question is, what has been the relative frequency of destructive fires versus fires that burn only part of the vegetation and leave behind substantial vegetation mosaics? This issue is relevant for the commonly held view that cutting cycles adopted in forestry ought to mimic the natural disturbance dynamics of forests (e.g., Harris 1984, Franklin & Forman 1987, Hunter 1990). This recommendation, although plausible, is insufficient because the average fire rotation does not reveal how much heterogeneity was left behind. I suspect that small-scale heterogeneity in managed areas is more critical for a large proportion of the forest fauna than the length of the cutting cycle per se.

(2) What proportion of forest has been untouched by fires? Is this important and if so, for how many organisms?

(3) To what extent have the ecological consequences of wildfires been modified by other 'environmental forcing functions' such as heavy winds and insect outbrakes (Holling 1992). By the term 'forcing function' (e.g., Huntley & Webb 1988, Delcourt & Delcourt 1991) I refer to externally triggered disturbances that modify local conditions frequently and regularly enough so that they are 'internalized' into the characteristics of the system, for instance into succession pathways (Haila & Levins 1992).

Another set of poorly explored questions relates to small-scale disturbances and mosaic-processes (Whittaker & Levin 1977) that occur independently of fires, possibly mainly in fire-refugia. For instance, the death of single trees creates small-scale disturbances and 'successions' on the level of single tree trunks, which create suitable microhabitats for particular suites of species such as fungi and insects. Are there other such 'micro-successional cycles' in the taiga in addition to or related to the decay of wood, for instance, in the litter decomposition system? How important is small-scale heterogeneity in soils, produced by plant growth (Pastor et al. 1987, Kuuluvainen et al. 1993, Kuuluvainen 1994) and annual variation in litter fall (Kouki & Hokkanen 1992), for different organisms?

Biotope continuity in a fairly small spatial scale may be a basic requirement for the maintanence of viable populations of species that depend on 'mosaic processes'. Such species live in niches that are ephemeral and need to be constantly reproduced within the dispersal radius of population members. Reproduction of such niches, on the other hand, depends on the character of the environment. The 'continuity' of, for instance, decaying deciduous wood required by specialized saproxylic beetles, is disrupted in intensively managed forests. Evidence supporting this statements comes from studies on threatened insects in Fennoscandia (Esseen et al. 1992, Siitonen & Martikainen 1994).

What is important in this context is the nature and interaction between different types of successional cycles in the taiga, and the whole suite of life-history strategies represented by the species adapted to these cycles. The overall nature of the successional cycle is probably determined by change in forest structure which is rapid in young stages but slows down later on, and this creates an interaction between changes in different time scales (Levandowsky & White 1977, Heinselman 1981, Haila & Levins 1992).

4. Data-based evaluations: where do we stand?

Overall, adequate quantitative data on the variation in distribution and abundance of forest organisms in different types of taiga and along the successional gradient are amazingly scarce. Long-term quantitative data collected over several decades are available basically only for game animals and Finnish birds. Forest insects are faunistically well known in Fennoscandia but, apart from economically significant pests, quantitative sampling started only in the 1980s. For instance, the review by Heliövaara & Väisänen (1984) on the effect of forestry on insects included hardly any references to quantitative data. In other parts of the boreal zone the situation is far less satisfactory. Less than half of the insects of Canada are taxonomically known (McLeod 1980), and vast tracts of Siberia are practically terra incognita as far as invertebrate assemblages go.

This unfortunate situation is exacerbated by two historical burdens. First, ecology, particularly animal ecology, has been neglected within forestry science, which in the last decades has largely monopolized research on forests. Second, gross undervaluation of quantitative descriptive data, stemming from unnecessarily narrow and prescriptive views on ecological methods, has been a characteristic of modern ecology (Haila 1992, Haila & Levins 1992).

From the scarcity of adequate data it follows that assessments of the effect of forestry on taiga organisms must rest on broad and qualitative arguments. Partially these arguments are derived from general ecological characteristics of the taiga environment. In the following I discuss some generalizations supported by factual evidence and specify further problems that are in need of empirical scrutiny.

Habitat distribution patterns

The taiga has undergone an extremely dynamic history on several time scales. This suggests that successful taiga organisms are not very restrictive in their overall habitat requirements. Such seems to be the case: dominant species of, for instance, birds and carabid beetles in Finland occur in a wide spectrum of boreal forest biotopes, both in terms of tree species composition and in terms of stand age (Haila et al. 1994). Where forests are hetogeneous and patches are small, in the order of 5–20 ha as in southern Finland, a large proportion of forest birds and carabids fare well (Haila et al. 1987, Raivio & Haila 1990, Niemelä et al. 1988). However, different groups of organisms respond to different characteristics of forest. For many species of birds, the proportion of deciduous trees is a very important characteristic on the stand level (Angelstam 1992). Small-scale abundance variation of carabids, on the other hand, is greatly influenced by litter composition (Niemelä et al. 1992). Ultimately, such relationships between habitat features and the fauna ought to be demonstrated on the level of autecology; a good example is the dependence of Hazel hen (*Tetrastes bonasia*) on alder (Swenson 1993).

Mosaic patterns are probably very important in the habitat selection of taiga animals which often require a particular combination of habitat patches rather than pure stands. The notion of 'minimum habitat requirements' refers to such a combination of habitat elements that is sufficient for individuals of different species for successful reproduction, and seems useful in assessing habitat quality locally (Haila et al. 1989, 1994, Raivio 1992). Mosaic patterns are typical of the habitat of many taiga mammals as well (Hansson 1979).

Furthermore, there are changes in habitat occupancy through the annual cycle. These are commonplace for most birds of the taiga that are migrants or perform large-scale 'irruptive' movements. Also, many invertebrates probably move between biotopes during the year and in different stages of the life cycle, but data to support this expectation are insufficient (Esseen et al. 1992).

Young stands vs. old-growth

Although numerically dominant species of the taiga occur over a wide range of biotopes, there is clear faunal differentiation between old-growth and young, open forest stands. Species richness in carabids, ants and spiders is higher in young stages than in old-growth (Niemelä et al. 1988, 1993, Punttila et al. 1991, Pajunen 1986), which is understandable due to the higher variation in field layer vegetation. As the richness of field layer vegetation decreases with forest age (Esseen et al. 1992, Tonteri 1994), the same pattern is most probably true of the herbivorous fauna as well (Brown 1986).

A set of species are specialists of old-growth forests. Their proportion among birds and carabids in Finland is on the order of 5–10% of the species (Raivio & Haila 1990, Niemelä et al. 1988). This is, however, certainly too low an estimate for taxa specialized on decaying wood (Väisänen et al. 1993). On the other hand, young, open forest biotopes also have their typical specialized species, for instance hunting spiders (Huhta 1965, Pajunen 1986, McIver et al. 1992) and several species of carabids (Niemelä et al. 1993) and ants (Punttila et al. 1991). It is well known that recently burned forests have a large, specialized insect fauna (Esseen et al. 1992, Muona & Rutanen 1994).

There is evidence that species of young successional stages are good dispersers and colonize new clear-cuts within a couple of years after the cut (Haila et al. 1994). For instance, the spatial population structure of carabids in young successional stages in Finland, evaluated indirectly on the basis of individual movement patterns, seems extremely versatile (Harri Tukia, in preparation).

The significance of "communities"

"Community", understood as a unit structured by interspecific interactions, is a very problematic concept in the taiga. Dominant plants have their characteristic herbivorous fauna, and other obligatory species-to-species relationships can, of course, be identified, but by and large, local animal assemblages seem to be epiphenomena. A major exception is the community of ants, structured by competitive interactions in old-growth forests (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, Punttila et al. 1994a, 1994b). Ants have also a strong influence on other components of the ground fauna (Punttila 1994).

The significance of "micro-ecosystems"

Although taiga organisms do not fit into tightly structured communities, they can certainly be divided into 'subsystems' according to the character of the part of the wood web they are dependent upon. Some dependencies are obvious, for instance, the link of herbivores to their host plant and predators to their main prey, but a more challenging task would be to identify sets of interdependent, specialized species constituting small ecosystems that occur only in fairly specific circumstances. Species living on decaying wood or fungi form such 'subsystems' (e.g., Swift 1982, Esseen et al. 1992, Kaila et al. 1994). The boundary of the wood-fungus-fungivore-predator/parasitoid system is fuzzy because the set of species includes predators that are not dependent on this particular system (Kaila et al. 1994). Nevertheless, 'micro-ecosystems' typical of particular taiga environments have great analytic potential as indicators of taiga environments on a small scale. A pertinent question is, for instance, how many different types of systems live on decaying wood (Kaila et al. 1994)? Also, specialized mosses belong to distinct 'micro-ecosystems' and have similar diagnostic potential (Watson 1980, Söderström 1988).

Changes in forest structure

Changes in the proportional area occupied by different types of forests on the regional scale is a major consequence of forestry, as was recently demonstrated by Mladenoff et al. (1993); see also Syrjänen et al. (1994). Long-term census data have documented the consequences of such change on the distribution and abundance of forest birds in Finland (Järvinen & Väisänen 1977, 1978, Järvinen et al. 1977, Virkkala 1987, 1991a). The causal chain is not unambiguous, however. Forest type proportions have changed simultaneously with a through-going change in habitat structure that gets regional significance once it occurs consistently over a large enough area, although locally it may be almost undetectable. That fairly subtle changes in habitat structure are important is the conclusion reached by Lars von Haartman (1973, 1978) and Olli Järvinen with his coworkers (see Järvinen & Väisänen 1976, 1977, Järvinen et al. 1977, Haila et al. 1980, Helle & Järvinen 1986). Unfortunately, there is no way of drawing a sharp distinction between the effects of these two factors, that is, changes in forest type proportions and changes in the internal structure of stands, because they have everywhere occurred together.

The need is to investigate, and understand, factors that cause populations to decline before they become actually threatened (Caughley 1994). A systematic, uniform change in habitat structure is a plausible explanation for such secular trends. An analogue is the study of Stjernberg (1979) on the dramatic increase of the Rosefinch (*Carpodacus erythrinus*) in Finland in the 1950s and 1960s. Stjernberg concluded that the population increase was due to improved breeding success triggered by a systematic increase in bush density in habitats favoured by this species.

The significance of "fragmentation"

"Fragmentation", understood as a straightforward change of a particular environment from a 'more continuous' to a 'less continuous' state seems to be a secondary factor in the taiga. I derive this assumption from two kinds of evidence: First, the ecological systems of the taiga have been shaped by recurring disturbances which have created a continuously shifting mosaic of different forest types. Consequently, animals adapted to the taiga environment are also adapted to finding new suitable sites whenever the local environment deteriorates. Second, the animals of the taiga seem to require combinations of habitats on a fairly small scale rather than large, uniform forest stands. Thus, variable mosaic-likeness rather than continuous uniformity seems to be favourable for taiga animals. But, of course, habitat loss is a different issue and profoundly relevant for old-growth specialists, or species requiring a particular type of habitat mosaic such as the Capercaillie (*Tetrao urogallus*) (Rolstad & Wegge 1987, Lindén & Pasanen 1987).

However, an overtly typological view of 'fragmentation' is too restrictive. 'Fragmentation' can be used as a generic term for such changes in habitat configurations which bring about increasing isolation of patches from one another and/or new interactions between different habitat types (e.g., Usher 1987, Wiens 1990, Saunders et al. 1991, Haila et al. 1993). Changes in forest structure brought about by intensive management increase the isolation of patches of particular habitats from each other. This may be critical, for instance, for species that require biotope continuity: 'fragmentation' occurs whenever 'continuity' is disrupted and has, thus, spatial, temporal and species-behavioural elements. Also indirect effects such as an elevated predation rate in remaining old-growth stands caused by predators primarily living in the surrounding matrix of managed forests may be important. This has been documented in predominantly agricultural landscapes on the southern border of the Swedish taiga (Andrén et al. 1985, Andrén & Angelstam 1988), as well as in southern Norwegian forests (Rolstad & Wegge 1989), but the generalizability of these results to cutting mosaics in more northern parts of the taiga is an open issue. It is obvious, however, that more data are needed to assess indirect effects of forest fragmentation.

5. Research priorities

Our qualitative understanding of the basic ecology of the taiga is fairly reliable, but there is a great need for detailed knowledge on distribution and abundance patterns of different species and on processes regulating those patterns. For practical conclusions, patterns may often have priority over processes; it is useless to draw conclusions from processes if there is no evidence that those processes are actually relevant in the system considered. In particular, patterns of natural variation ought to be known because they give a standard for evaluating variation observed in human-modified environments (Haila & Levins 1992, Haila et al. 1994). There is no reason to get concerned about variation that is perfectly natural in character and magnitude: an assumption of 'natural balance' is an unrealistic baseline for assessing human influence. Very few studies have systematically assessed the magnitude of natural variation in the taiga (Haila et al. 1994); an outstanding exception is Virkkala's (1989, 1991b) comparison of annual variation in numbers of breeding birds in Finnish Lapland in managed forests and in large preserves: he found that large-scale environmental effects tended to synchronize fluctuations across biotopes, but a set of taiga specialists fluctuated more in managed than in natural forests.

In the following I make a few suggestions on research priorities without repeating specific points already made above.

(1) As is true more generally in conservation ecology, there is a great need for systematic survey work: one should know what the 'biodiversity' of the taiga consists of, and where it is, before suggesting practical measures (Margules & Nicholls 1987, Margules et al. 1988, Margules & Austin 1991). Surveys are needed on a large biogeographic scale for detecting gradients in abundance variation of single species, of assemblage composition, and of genetic composition. Descriptive surveys should include an analytic edge so that the results could be used for evaluating underlying conceptual assumptions (Haila 1988, 1992, Margules & Austin 1991). A particular challenge is to distinguish between human-caused changes and systematic change

across natural gradients. This is important for instance in the western Palearctic: it seems attractive to use the northern Russian taiga as a model for primeval Fennoscandian forests, but this is problematic because of clinal variation in critical environmental variables.

(2) Presence–absence data, if systematically collected, are fruitful for assessing distribution patterns, but research on variation requires quantitative data. This creates several further questions. There is no universal method for collecting quantitative ecological samples, but only particular, more or less satisfactory, methods for sampling or censusing particular types of organisms. A problem that always makes the interpretation of sampling results difficult is, what is the 'universe' sampled, that is, which species belong to the pool that is actually subjected to sampling? The bulk of the species consists of relatively common, generalized species, and the scarcer ones may be only accidentally included. Are these 'accidents' evenly distributed in a statistical sense, or are they dependent upon the location of traps relative to, for instance, particular microhabitats? The composition of the universe depends on variation in the environment, thus, a systematic sampling design is necessary (Margules & Austin 1991). A further problem is that the 'universe' probably expands with time, i.e., the overall pool of species caught increases because of population fluctuations and temporary migrations (Williams 1964). Relevant changes should be distinguished from more transitory ones.

Rare species are only occasionally caught in general sampling schemes, because of their specialized habits. The absence of specialized species from samples is not a reliable indicator of true absence, because an expectation from metapopulation theory is that a species may be temporarily absent from sites that are necessary for its permanent existence (Levins 1969, Gilpin & Hanski 1991). There is no substitute for good knowledge of the natural history and ecology of rare, specialized species. Such knowledge can be used to conduct focused, labour-intensive surveys of particular species groups such as insects living on decaying wood (e.g., Siitonen & Martikainen 1994).

(3) The question what to sample depends on the particular purpose of each study. For instance, the following alternatives could be tried for evaluating the quality of the environment on the basis of survey data: (1) microecosystems characteristic of particular taiga environments (as discussed above); (2) typical species of the taiga, defined on biogeographic criteria (as discussed above); or (3) particularly selected, moderately abundant species that respond to environmental changes in different characteristic scales (Virkkala 1991b, Haila et al. 1994). Systematic assessments of the value of these surrogates, and potential alternatives, are greatly needed.

(4) Surveys, by definition, record only individuals, but conclusions about the status of taiga fauna ought to be drawn on the population scale: population viability is the critical issue. Some possible ways to bridge the gap from survey results to populations are suggested in Haila et al. (1994). Ultimately, data are needed on variation in reproductive success of target species in forests modified to variable degrees (e.g., Virkkala 1990), preferably obtained by replicated experiments.

(5) Although the traditional concept of 'community', tightly structured by interspecific interactions, is suspect in the taiga, other types of interactions need more attention than they have received, particularly the relationships between mosaic patterns and ecosystem function. Some relationships are well established, for instance, key herbivores such as the moose (*Alces alces*) influence regeneration of trees and herbs (Pastor et al. 1988, Pastor & Naiman 1992) which in turn determine litter output to soil, and litter quality has a significant effect on the soil fauna (Huhta et al. 1967). Elaboration of this aspect of forest ecology opens up possibilities for experimental work and laboratory microcosms studies, for instance on relationships within the detritus food web. This question is also relevant for maintaining productivity of forest soils.

6. Management implications: optimism vs. pessimism?

Timber production is not a sufficient criterion of ecological sustainability of forest management. However, although preservation of 'biodiversity' is accepted as an important element in ecological sustainability, ambiguities remain because 'biodiversity' is difficult to operationalize in research (Haila & Kouki 1994). Preservation of species is probably the least ambiguous single criterion, and it covers also aspects of environmental diversity because preservation of species requires preservation of a variety of environments (Margules et al. 1988, 1993).

I suggest that the following three issues should be held separate when discussing ways to achieve sustainability in forest management:

1) definition of goals,
2) formulation of recommendations derived from these goals in such a way that they are operationalizable, i.e., conducive to practical conclusions that can be implemented, and
3) definition of criteria that allow monitoring of success or failure.

It seems that the general goal of 'preserving biodiversity' differentiates into more specific recommendations roughly according to major spatial scales, namely, biogeographic, regional, and local. Crucial issues to be resolved in these three scales are, schematically, as follows: representativeness of the reserve system (biogeographic scale), area proportions of different forest types and age classes (regional scale), and heterogeneity of forest types between and within stands in the forest landscape (local scale). In addition, it is necessary to develop recommendations concerning actual cutting operations: which stands, snags, bushes, small wetlands etc. should be left intact?

This scheme is an idealization, but it has the advantage that corresponding administrative organizations already exist. The particular responsibilities of these organizations should be differentiated from each other. Thus, the scheme opens potential prospects for fruitful interactions between ecologists and forest managers on specified issues instead of fruitless arguments about general, non-operationalizable principles. A problem in environmental debates often is that no practical conclusions follow from general and abstract goals such as 'preservation of biodiversity' if they are not further specified.

I do not repeat suggestions and recommendations concerning forest management practices presented by, for instance, several authors in Hansson (1992) and in this volume, but conclude with four general points.

(1) Representativeness of existing reserves, and the need for new ones, should be assessed systematically all over the taiga (Margules et al. 1988, 1993). Such an assessment should also focus on disturbance regimes that maintain particular biotic patterns (Pickett & Thompson 1978), not only large-scale wildfires but all factors affecting forest stand dynamics (Angelstam & Holmer 1993, Syrjänen et al. 1994). Thus, it is necessary to consider also forest history.

(2) The decisive question, however, is the fate of managed forests. This really divides into two issues: between stand heterogeneity (and representativeness on the regional scale), and within stand composition and structure. The changes caused by forestry in forest type configurations ought to be planned (Franklin & Forman 1987). Such plans could be made using similar systematic mehods as in selecting a reserve network, although the areas included need not be reserves but just different types of forest: the issue is to ensure different forest types are left in appropriate area proportions. A certain circularity remains, however, in such an exercise, as pointed out by Belbin (1993), as evaluations need to be backed by ecological data. An issue requiring particular attention is the type and amount of heterogeneity that should be maintained in managed forests. Microhabitats necessary for selected target organisms and 'microecosystems' require special attention.

Recommendations derived from rules of thumb that are probably quite reasonable have been developed in northern Europe since the 1970s (Esseen et al. 1992). These need implementation, but a particular priority is to monitor systematically their success or failure.

(3) In some parts of the taiga, for instance in southern Fennoscandia, most of the forests are subjected to intensive management and the proportion of preserved old-growth is very small. In such a situation restoration is an imminent challenge. Fire is a good tool, as suggested by recent burning experiments in southern Finland (unpublished data, collected by several specialistis on different taxa; see also Muona & Rutanen 1994). Large-scale disturbance cycles give a good

model for wilderness management (Wright 1974) but the advice is more problematic as a management guideline, for reasons I already mentioned and also because exceptional fires cannot be reproduced (Hunter 1993). However, knowledge of natural disturbance gives models for restoration.

(4) By and large, the possibilities of matching together forest management and conservation requirements in the taiga seem good. The taiga is a resilient ecological system, naturally adapted to disturbances that can be reasonably well mimicked by management operations, and thus easier to manage than many other forested biomes. This is also the basis for the achieved sustainability of timber production (Hunter 1990, Kuusela 1990). A priori reasoning supports a similar conclusion: the taiga has recently and continuously undergone such 'natural catastrophes' and transformations that are comparable to the consequences of human activities.

Thus, I think the attitude reflected in the 'Taiga News' editorial cited in the introduction is too pessimistic. But although guidelines for sustainable forest management can be designed on paper, their implementation remains a serious challenge. Unproblematic optimism concerning future forest management would be irresponsible, particularly because of the many unknowns inherent in the probability of future global climate change.

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References

Andrén, H. & Angelstam, P. 1988: Elevated predation rates as an edge effect in habitat islands: experimental evidence. — Ecology 69:544–547.

Andrén, H., Angelstam, P., Lindström, E. & Widén, P. 1985: Differences in predation pressure in relation to habitat fragmentation: an experiment. — Oikos 45:273–277.

Angelstam, P. 1992: Conservation of communities – the importance of edges, surroundings and landscape mosaic structure. — In: Hansson, L. (ed.), Ecological principles in nature conservation: 9–70. Elsevier, London.

Angelstam, P. & Holmer, M. 1993: [Manage the whole landscape!] (In Swedish) — Skog och forskning 1993(1):4–12.

Åström, S. E. 1977: Natur och byte. — Söderströms. Helsingfors.

Barnosky, C. W. 1987: Response of vegetation to climatic changes of different duration in the late Neogene. — Trends Ecol. Evol. 2:247–250.

Bartlein, P. J. 1988: Late-tertiary and quaternary palaeoenvironments. — In: Huntley, B. & Webb, T. III (eds.), Vegetation history: 13–152. Kluwer Academic, Dordrecht.

Belbin, L. 1993: Environmental representativeness: regional partitioning and reserve selection. — Biol. Conserv. 66:223–230.

Birks, H. J. B. 1986: Late-Quaternary biotic changes in terrestrial lacustrine environments, with particular reference to north-west Europe. — In: Berglund, B. E. (ed.), Handbook of Holocene palaeoecology and palaeohydrology: 3–65. John Wiley & Sons, New York.

Bonan, G. B. & Shugart, H. H. 1989: Environmental factors and ecological processes in boreal forests. — Ann. Rev. Ecol. Syst. 20:1–28.

Brown, V. K. 1986: Life cycle strategies and plant succession. — In: Taylor, F. & Karban R. (eds.), The evolution of insect life cycles: 105–124. Springer-Verlag, New York.

Brubaker, L. B. 1975: Postglacial forest patterns associated with till and outwash in Northcentral Upper Michigan. — Quaternary Res. 5:499–527.

Brunov, B. B. (Брунов, Б. Б.) 1978: An experience in analyzing the faunistic groups of birds of the palearctic taiga. (In Russian with English summary) — Bjull. Mosk. o-va isp. prirody, otd. biol. 83:5–15.

— 1980: O nekatoryh faunisticheskih gruppah ptits tajgi Evrazii. (In Russian with English summary) — In: Voronov, A. G. & Drozdov, N. N. (eds.), Sovremennye problemy zoogeografii: 217–254. Nauka, Moscow.

Caughley, G. 1994: Directions in conservation biology. — J. Animal Ecology (in press).

Chernov, Y. (Чернов, Ю.) 1975: Prirodnaya zonalnost i zhivotnii mir sushi. [Zonality in nature and terrestrial animals] (In Russian) — Nauka, Moscow.

— 1985: The living tundra. — Cambridge University Press, Cambridge.

Delcourt, H. R. & Delcourt, P. A. 1991: Quaternary ecology. A paleoecological perspective. — Chapman & Hall, London.

Dolukhanov, P. M. & Khotinskiy, N. A. 1984: Human cultures and the natural environment in the USSR during the Mesolithic and Neolithic. — In: Velicho, A. A., Wright, H. E. Jr. & Barnosky, C. W. (eds.), Late Quaternary environments of the Soviet Union: 319–327. Longman, London.

Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992: Boreal forests — the focal habitats of Fennoscandia. — In: Hansson, L. (ed.), Ecological principles of nature conservation: 252–325. Elsevier, London.

Fox, J. F. 1983: Post-fire succession of small-mammal and bird communities. — In: Wein, R. W. & MacLean, D. A. (eds.), The role of fire in northern circumpolar ecosystems: 155–180. John Wiley & Sons, New York.

Franklin, J. F. & Forman, R. T. T. 1987: Creating landscape patterns by forest cutting: Ecological consequences and principles. — Landscape Ecol. 1:5–18.

von Haartman, L. 1973: Changes in the breeding bird fauna of North Europe. In: Breeding biology of birds: 448–481. — Nat. Acad. Sci. Washington DC.

— 1978: Changes in the bird fauna in Finland and their causes. — Fennia 150:25–32.

Haila, Y. 1985: Birds as a tool in reserve planning. — Ornis Fennica 62:96–100.

— 1988: The multiple faces of ecological theory and data. — Oikos 53:408–411.

— 1992: Measuring nature: quantitative data in field biology. — In: Clarke A. E. & Fujimura, J. H. (eds.), The right tools for the job. At work in twentieth-century life sciences: 233–253. Princeton Univ. Press, Princeton, N.J.

Haila, Y. & Järvinen, O. 1990: Northern conifer forests and their bird species assemblages. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 61–85. SPB Acad. Publishing, The Hague.

Haila, Y. & Kouki, J. 1994: The phenomenon of biodiversity in conservation biology. — Ann. Zool. Fennici 31:5–18.

Haila, Y. & Levins, R. 1992: Humanity and nature. Ecology, science and society. — Pluto Press, London.

Haila, Y., Järvinen, O. & Väisänen, R. A. 1980: Effects of changing forest structure on long-term trends in bird populations in SW Finland. — Ornis Scand. 11:12–22.

Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga, southern Finland. — Ornis Fennica 64:90–106.

— 1989: Methodology for studying minimum habitat requirements of forest birds. — Ann. Zool. Fennici 26:173–180.

Haila, Y., Saunders, D. & Hobbs, R. 1993: What do we presently understand about ecosystem fragmentation? — In: Saunders, D. A., Hobbs, R. J. & Ehrlich, P. (eds.), Nature conservation 3: Reconstruction of fragmented ecosystems: 45–55. Surrey Beatty & Sons, Chipping Noreton, NSW.

Haila, Y., Hanski, I. K., Niemelä, J., Punttila, P., Raivio, S. & Tukia, H. 1994: Forestry and the boreal fauna: matching management with natural forest dynamics. — Ann. Zool. Fennici 31:187–202.

Hansson, L. 1979: On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. — Oikos 33:182–189.

— 1992: Landscape ecology of boreal forests. — Trends Ecol. Evol. 7:299–302.

— ed.) 1992: Ecological principles of nature conservation. — Elsevier, London.

Hare, F. K. 1954: The boreal conifer zone. — Geogr. Stud. 1:4–18.

Hargrove, W. W. & Pickering, J. 1992: Pseudoreplication: a sine qua non for regional ecology. — Landscape Ecol. 6:251–258.

Harris, L. D. 1984: The fragmented forest: island biogeography theory and the preservation of biotic diversity. — Univ. of Chicago Press, Chicago.

Heinselman, M. L. 1981: Fire and succession in the conifer forests of northern North America. — In: West, D. C., Shugart, H. H. & Botkin, D. B. (eds.), Forest succession. Concepts and applications: 374–405. Springer-Verlag, New York.

Heliövaara, K. & Väisänen, R. 1984: Effects of modern forestry on northwestern European forest invertebrates: a synthesis. — Acta Forest. Fennici 189:1–32.

Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — Oikos 46:107–115.

Heusser, L. E. & King, J. E. 1988: North America. — In: Huntley, B. & Webb, T. III (eds.), Vegetation history: 193–236. Kluwer, Dordrecht.

Holling, C. S. 1992: The role of forest insects in structuring the boreal landscape — In: Shugart, H. H., Leemans, R. & Bonen, G. B. (eds.), A systems analysis of the global boreal forest: 170–191. Cambridge University Press, Cambridge.

Huhta, V. 1965: Ecology of spiders in the soil and litter of Finnish forests. — Ann. Zool. Fennici 2:260–308.

Huhta, V., Karppinen, E., Nurminen, M. & Valpas, A. 1967: Effect of silvicultural practicies upon arthopod, annelid and nematode populations in coniferous forest soil. — Ann. Zool. Fennici 4:87–143.

Hunter, M. L. Jr. 1990: Wildlife, forests, and forestry. Principles of managing forests for biological diversity. — Prentice Hall, Englewood Cliffs, NJ.

— 1993: Natural fire regimes as spatial models for managing boreal forests. — Biol. Conserv. 65:115–120.

Huntley, B. & Webb, T. III 1988: Discussion. — In: Huntley, B. & Webb, T. III (eds.), Vegetation history: 780–785. Kluwer Academic, Dordrecht.

— (eds.) 1988: Vegetation history. — Kluwer, Dordrecht.

Hustich, I. 1974: Common species in the northern part of the Boreal Region of Canada. An essay. — Rep. Kevo Subarctic Res. Stat. 11:35–41.

Hämet-Ahti, L. 1981: The boreal zone and its biotic subdivisions. — Fennia 159:69–75.

Imbrie, J. & Imbrie, K. P. 1979: Ice ages: solving the mystery. — Enslow Publishers, Short Hills, NJ.

Järvinen, O. & Väisänen, R. A. 1977: Recent quantitative changes in the populations of Finnish land birds. — Polish Ecol. Stud. 3(4):177–188.

— 1978: Long-term population changes in the most abundant south Finnish forest birds during the past 50 years. — J. Ornithol. 119:441–449.

— 1979: Changes in bird populations as criteria of environmental changes. — Holarct. Ecol. 2:75–80.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. — Silva Fennica 11:284–294.

Kaila, L., Martikainen, P., Punttila, P. & Jakovlev, E. & 1994: Saproxylic beetles on dead birch trunks: effect of polypore species decaying the trunk. — Ann. Zool. Fennici 31:97–107.

Keast, A. 1990: Biogeography of the North American broad-leafed deciduous forest avifauna. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 109–120. SPB Academic Publishing, The Hague.

Kouki, J. & Hokkanen, T. 1992: Long-term needle litterfall of a Scots pine Pinus sylvestris stand: relation to temperature factors. — Oecologia (Berlin) 89:176–181.

Kullman, L. 1991: Pattern and process of present tree-limits in the Tärna region, southern Swedish Lapland. — Fennia 169:25–38.

Kullman, L. & Engelmark, O. 1991: Historical biogeography of Picea abies (L.) Karst. at its subarctic limit in northern Sweden. — J. Biogeography 18:63–70.

Kuuluvainen, T. 1994: Regeneration patterns of boreal coniferous forest in relation to gap disturbance and ground microtopography: a review and discussion of observations in Finland. — Ann. Zool. Fennici 31:35–51.

Kuuluvainen, T., Hokkanen, T. J., Järvinen, E. & Pukkala, T. 1993: Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of vegetation-soil system. — Can. J. Forestry (in press).

Kuusela, K. 1990: The dynamics of boreal coniferous forests. — SITRA, Helsinki.

Levandowsky, W. & White, B. S. 1977: Randomness, time scales, and the evolution of biological communities. — Evol. Biology 15:69–161.

Lindén, H. & Pasanen, J. 1987: Capercaillie leks are threatened by forest fragmentation. (In Finnish with English summary) — Suomen Riista 34:66–76.

Loucks, O. L. 1970: Evolution of diversity, efficiency, and community stability. — Amer. Zool. 10:17–25.

McIver, J. D., Parsons, G. L. & Moldenke, A. R. 1992: Litter spider succession after clear-cutting in western coniferous forest. — Can. J. Forest Res. 22:984–992.

McLeod, J. M. 1980: Forests, disturbances, and insects. — Can. Entomol. 112:1185–1192.

Makaev, Y. A. (Макаев, Ю. А.) 1987: Zoogeograficheskie kompleksy Evrazii. [Zoogeographic formations in Eurasia] (In Russian) — Nauka, Leningrad.

Margules, C. R. & Nicholls, A. O. 1987: Assessing the conservation value of remnant habitat 'islands' mallee patches on the western Eyre Peninsula, South Australia. — In: Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M. (eds.), Nature conservation: the role of remnants of native vegetation: 89–102. Surrey Beatty & Sons, Chipping Norton, NSW.

Margules, C. R., Nicholls, A. O. & Pressey, R. L. 1988: Selecting networks of reserves to maximize biological diversity. — Biol. Conserv. 43:63–76.

Margules, C. R., Cresswell, I. D. & Nicholls, A. O. 1993: A scientific basis for establishing networks of protected areas. — In: Forey, P. L., Humpries, C. J. & Vane-Wright, R. I. (eds.), Systematics and conservation evaluation. Oxford University Press, Oxford (in press).

Margules, C. R. & Austin, M. P. (eds.) 1991: Nature conservation: cost effective biological surveys and data analysis. — CSIRO Publ., East Melbourne, Victoria.

Matjushkin, E. N. (Матюшкин, З. Н.) 1982: [Regional differentiation of the Palearctic fauna in the past and in the present] (In Russian) — In: Drozdov, N. N., Maksimova, V. F., Mjalo, E. G. & Sokolov, I. A. (Дроздов, Н. Н., Максимова, В. Ф., Мяло, Е. Г. & Соколов, И. А.) (eds.), Teoreticheskie i prikladnye aspekty biogeografii [Theoretical and applied aspects of biogeography]: 59–80. Nauka. Moscow.

Mayr, E. 1976: History of the North American bird fauna. — In: Mayr, E. (ed.), Evolution and the diversity of life: 565–588. Belknap Press, Cambridge, Mass.

Mladenoff, D. J. & Pastor, J. 1993: Sustainable forest ecosystems in the northern hardwood and conifer region: concepts and management. — In: Olson, J. T., Sample, V. A. & Johnson, H. (eds.), Defining sustainable forestry. Island Press, Washington DC.

Mladenoff, D., White, M. A., Pastor, J. & Crow, T. R. 1993: Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. — Ecol. Applic. 3:294–306.

Mönkkönen, M. 1994: Diversity in Nearctic and Palearctic forest bird assemblages. (In Finnish with English summary) — Forest Research Institute Research Papers (in press).

Mönkkönen, M. & Helle, P. 1989: Migratory habits of birds breeding in different stages of forest succession: a comparison between the Palearctic and the Nearctic. — Ann. Zool. Fennici 26:323–330.

Mönkkönen, M. & Welsh, D. 1994: Biogeographical insights on the effects of human caused landscape changes on the forest bird communities of Europe and North America. — Ann. Zool. Fennici 31:61–70.

Muona, J. & Rutanen, I. 1994: The shorth term impact of fire on the beetle fauna in boreal coniferous forest. — Ann. Zool. Fennici 31:109–121.

Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. 1988: The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forests. — Ann. Zool. Fennici 25:107–119.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1992: Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. — J. Biogeogr. 19:173–181.

Niemelä, J., Spence, J. R., Langor, D., Haila, Y. & Tukia, H. 1994: Logging and boreal ground-beetle assemblages on two continents: implications for conservation. — In: Gaston, K., Samways, M. & New, T. (eds.), Perspectives in insect conservation. Intercept Publications, Andover (in press).

Niemelä, P. & Mattson, W. J. 1992: Invasion of North American forests by European phytophagous insects: why so many? — In: American forestry – an evolving tradition. Proc. 1992 Soc. American Foresters National Convention: 202–208. Soc. American Foresters, Bethesda, Maryland.

Nikolov, N. & Helmisaari, H. 1992: Silvics of the circumpolar boreal forest tree species. — In: Shugart, H. H., Leemans, R. & Bonan, G. B. (eds.), A systems analysis of the global boreal forest: 13–84. Cambridge University Press, Cambridge.

Pastor, J. & Naiman, R. J. 1992: Selective foraging and ecosystem processes in boreal forests. — Amer. Nat. 139:223–230.

Pastor, J., Gardner, R. H., Dale, V. H. & Post, W. M. 1987: Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. — Can. J. Forest Res. 17:1394–1400.

Pastor, J., Naiman, R. J., Dewey, B. & McInnes, P. 1988: Moose, microbes and the boreal forest. — BioScience 38:770–777.

Payette, S. 1992: Fire as a controlling process in North American boreal forest. — In: Shugart, H. H., Leemans, R. & Bonan, G. B. (eds.), A systems analysis of the global boreal forest: 144–169. Cambridge University Press, Cambridge.

Pickett, S. T. A. & Thompson, J. N. 1978: Patch dynamics and the design of nature reserves. — Biol. Conserv. 13:27–37.

Punttila, P. 1994: Wood ants and the structure of arthropod communities in the taiga. (In Finnish with English summary) — Forest Research Institute Research Papers (in press).

Punttila, P., Haila, Y., Pajunen, T. & Tukia, H. 1991: Colonization of clearcut forests by ants in the southern Finnish taiga: a quantitative survey. — Oikos 62:250–262.

Punttila, P., Haila, Y., Niemelä, J. & Pajunen, T. 1994a: Ant communities in fragments of old-growth taiga and managed surroundings. — Ann. Zool. Fennici 31:131–144.

Punttila, P., Haila, Y. & Tukia, H. 1994b: Ant communities in clearcut southern Finnish taiga forest: habitat effects and species interactions. — Oikos (submitted).

Radkau, J. 1983: Holzverknappung und Krisenbewusstsein im 18. Jahrhundert. — Geschichte und Gesellschaft 9:513–543.

Radkau, J. & Schäfer, I. 1987: Holz. Ein Naturstoff in der Technikgeschichte. — Rowohlt, Reinbek bei Hamburg.

Raivio, S. 1992: Bird communities in fragmented coniferous forests: the importance of quantitative data and adequate scaling. — Ph.D. thesis, Dept. Zool., Univ. Helsinki.

Raivio, S. & Haila, Y. 1990: Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season. — Ornis Fennica 67:73–83.

Rassi, P. & Väisänen, R. 1987: Threatened animals and plants in Finland. English summary of the report of the Committee for the Conservation of Threatened Animals and Plants in Finland. — Ministry of the Environment, Helsinki.

Rolstad, J. & Wegge, P. 1987: Distribution and size of capercaillie leks in relation to old forest fragmentation. — Oecologia (Berl.) 72:389–394.

— 1989: Capercaillie Tetrao urogallus populations and modern forestry — a case for landscape ecological studies. — Finnish Game Res. 46:43–52.

Savolainen, R. & Vepsäläinen, K. 1988: A competitive hierarchy among boreal ants: impact on resource partitioning and community structure. — Oikos 51:135–155.

Shugart, H. H. 1984: A theory of forest dynamics. The ecological implications of forest succession models. — Springer Verlag, New York ,Heidelberg, Tokyo.

Siitonen, J. & Martikainen, P. 1994: Occurrence of rare and threatened insects living on decaying Populus tremula: a comparison between Finnish and Russian Karelia. — Scand. J. Forest Res. (in press).

Shugart, H. H., Leemans, R. & Bonan, G. B. (eds.) 1992: A systems analysis of the global boreal forest. — Cambridge University Press, Cambridge.

Solomon, A. M. 1992: The nature and distribution of past, present and future boreal forests: lessons for research and modeling agenda. — In: Shugart, H. H., Leemans, R. & Bonan, G. B. (eds.), A systems analysis of the global boreal forest: 291–307. Cambridge University Press, Cambridge.

Spicer, R. A. & Chapman, J. L. 1990: Climate change and the evolution of high-latitude terrestrial vegetation and floras. — Trends Ecol. Evol. 5:279–284.

Sprugel, D. G. 1991: Disturbance, equilibrium, and environmental variability: What is 'natural' vegetation in a changing environment? — Biol. Conserv. 58:1–18.

Stegman, B. K. (Штегман, Б. К.) 1938: Osnovy ornitogeograficheskogo delenija Palearktiki. (Zusammenfassung: Grunzüge der ornithogeografischen Gliederung des palearktischen Gebietes.) — Fauna SSSR. Ptitsy. Tom 1, vyp. 2. Izd-vo Akad. Nauk SSSR. Moskva-Leningrad.

Stjernberg, T. 1979: Breeding biology and population dynamics of the scarlet rosefinch Carpodacus erythrinus. — Acta Zool. Fennica 157:1–88.

Swenson, J. E. 1993: The importance of alder to hazel grouse in Fennoscandian boreal forest: evidence from four levels of scale. — Ecography 16:37–46.

Swift, M. J. 1982: Basidiomycetes as components of forest ecosystems. — In: Frankland, J. C., Hedger, J. N. & Swift, M. J. (eds.), Decomposer basidiomycetes: their biology and ecology: 307–337. Cambridge University Press, Cambridge.

Syrjänen, K., Kalliola, R., Puolasmaa, A. & Mattsson, J. 1994: Landscape structure and forest dynamics in subcontinental Russian European taiga. — Ann. Zool. Fennici 31:19–34.

Söderström, L. 1988: The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. — Biol. Conserv. 45:169–78.

Tonteri, T. 1994: Species richness of boreal understorey forest vegetation in relation to site type and successional factors. — Ann. Zool. Fennici 31:53–60.

Tuhkanen, S. 1984: A circumboreal system of climatic-phytogeographical regions. — Acta Bot. Fennica 127:1–50.

Usher, M. B. 1987: Effects of fragmentation on communities and populations: actions, reactions and applications to wildlife consrvation. — In: Saunders, D. A., Arnold, D. W., Burbridge, A. A. & Hopkins, A. J. M. (eds.), Nature conservation: the role of remnants of native vegetation: 103–21. Surrey Beatty & Sons, Chipping Norton, NSW.

Velicho, A. A., Wright, H. E. Jr. & Barnosky, C. W. (eds.) 1984: Late Quaternary environments of the Soviet Union. — University of Minnesota Press, Minneapolis, Minnesota.

Vepsäläinen, K. & Pisarski, B. 1982: Assembly of island ant communities. — Ann. Zool. Fennici 19:327–338.

Virkkala, R. 1987: Effects of forest management on birds breeding in northern Finland. — Ann. Zool. Fennici 24:281–294.

— 1989: Short-term fluctuations of bird communities and populations in virgin and managed forests in northern Finland. — Ann. Zool. Fennici 26:277–285.

— 1990: Ecology of the Siberian tit Parus cinctus in relation to habitat quality: effects of forest management. — Ornis Scand. 21:139–146.

— 1991a: Population trends of forest birds in Finnish Lapland in a landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? — Biol. Conserv. 56:223–240.

— 1991b: Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. — Oikos 62:59–66.

Väisänen, R., Biström, O. & Heliövaara, K. 1993: Subcortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? — Biodiversity Conserv. 2:95–113.

Watson, M. A. 1980: Patterns of habitat occupation by mosses — relevance to considerations of the niche. — Bull. Torrey Bot. Club 107:346–372.

Watts, W. A. 1988: Europe. — In: Huntley, B. & Webb, T. III (eds.), Vegetation history: 155–192. Kluwer Academic, Dordrecht.

Wein, R. W. & El-Bayoumi, M. A. 1983: Limitations to predictability of plant succession in northern ecosystems. — In: Wein, R. W., Riewe, R. R. & Methven, I. R. (eds.), Resources and dynamics of the boreal zone: 214–225. Association of Canadian Universities for Northern Studies, Ottawa.

Wein, R. W. & MacLean, D. A. 1983: An overview of fire in northern ecosystems. — In: Wein, R. W. & MacLean, D. A. (eds.), The role of fire in northern circumpolar ecosystems: 1–18. John Wiley & Sons, New York.

West, R. G. 1977: Pleistocene geology and biology. — Longman, London.

Whittaker, R. H. & Levin, S. A. 1977: The role of mosaic phenomena in natural communities. — Theor. Popul. Biol. 12:117–139.

Wiens, J. A. 1990: Habitat fragmentation and wildlife populations: the importance of autecology, time, and landscape stucture. — Trans. 19th IUGB Congr., Trondheim 1989: 381–391.

Williams, C. B. 1964: Patterns in the balance of nature. — Acad. Press, London.

Wright, H. E. Jr. 1974: Landscape development, forest fires, and wilderness management. — Science 186:487–495.