



Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland

Jari Kouki*, Kerstin Arnold, Petri Martikainen

Faculty of Forest Sciences, University of Joensuu, P.O. Box 111, Joensuu FIN-80101, Finland

Received 10 December 2002; accepted 5 August 2003

KEYWORDS

Boreal forests;
Fennoscandia;
Forest succession;
Populus tremula;
Moose *Alces alces*;
Threatened species

Summary

Large, dead and dying European aspens (*Populus tremula* L.) host many threatened species in Fennoscandian boreal forests. Large aspen trees have mostly disappeared and are being harvested from the managed forests that cover 95% of the forest area in Finland. Due to the small area protected (4.1%), the aspen-associated species may encounter major difficulties in the protected areas if aspen trees disappear due to natural forest succession. The availability of aspens was assessed in the old-growth conservation area network in eastern Finland. We mapped all the living and dead aspens in 15 protected old-growth forests. The total number of counted trees was 32 903 individuals. Current amounts of living ($2.7\text{ m}^3/\text{ha}$) and especially dead aspens ($2.8\text{ m}^3/\text{ha}$) in the protected areas were higher than in the surrounding managed forests (1.1 and $0.1\text{ m}^3/\text{ha}$ for living and dead trees, respectively). However, while saplings ($\text{dbh} < 5\text{ cm}$) occur in most of the areas (12 individuals/ha on average) they survive poorly and young aspen cohorts ($5\text{ cm} < \text{dbh} < 15\text{ cm}$) are lacking or are very rare. The most likely reason for the poor sapling survival is high browsing pressure by the mammalian herbivores, especially the moose. The moose population has increased many times in Finland during the past decades. The poor regeneration of aspens implies that the value of the old-growth conservation areas for aspen-associated species will face a serious bottleneck within a few decades when the currently middle-aged tree cohorts disappear. If the current high browsing pressure and lack of natural disturbances continue the obligatory aspen-associated species may disappear both locally and regionally from the network of the protected areas.

© 2004 Elsevier GmbH. All rights reserved.

*Corresponding author. Fax: +358-13-251-4444.

E-mail address: jari.kouki@joensuu.fi (J. Kouki).

Introduction

Establishment of protected areas is one of the key tools to alleviate the negative consequences that human influence has on natural biota. The conservation areas are often small and occur as fragmented patches in the midst of modified habitats. Studies on the spatial dynamics of populations have provided ample theoretical evidence that long-term persistence of species may be seriously impaired in highly fragmented habitats (Hanski, 1998, 1999; Hasting & Harrison, 1994; Tilman & Kareiva, 1997).

The ecological reasons and mechanisms that cause local and regional extinctions are often assumed to be caused by purely stochastic factors that are related to small population size. However, extinctions in fragmented habitats may also be related to changes in habitat availability and quality in the fragments in addition to stochastic factors (Harrison, 1994; Harrison & Bruna, 1999; Johst, Brandl, & Eber, 2002; Keymer, Marquet, Velasco-Hernandez, & Levin, 2000; Stelter, Reich, Grimm, & Wissel, 1997; Thomas, 1994; Thomas & Hanski, 1997).

Many ecosystems and protected areas are indeed characterised by internal habitat dynamics that can quite rapidly change their ecological properties (Borman & Likens, 1979; Paine & Levin, 1981; Remmert, 1991; Stelter et al., 1997; Thomas, 1994). Boreal forests, for example, are typically driven by natural disturbance dynamics that create and maintain their structural properties and successional patterns (e.g. Bonan & Shugart, 1989; Maarel, 1993). Although the internal dynamics may spread over relatively long time spans (10–100 years), ecosystem change is inevitable at the patch and forest stand scale. Some of the changes can be quite rapid, while others may take decades or even centuries to become visible (Esseen, Ehnström, Ericson, & Sjöberg, 1997; Hofgaard, 1993; Niklasson & Granström, 2000; Uotila, Kouki, Kontkanen, & Pulkkinen, 2002). When forest succession proceeds in protected areas, species adapted to discontinuous habitats may face the risk of local extinction, and hence the capacity of the protected areas to save the species is reduced.

Recent assessment of Finnish biota classified about 250 of the species that occur on mineral soil forests as threatened, and almost 150 of these are old-growth forests-dwellers (Anon, 2000; Rassi, Alanen, Kanerva, & Mannerkoski, 2001). During the last decade a protection programme for saving the valuable old-growth areas was launched in Finland (Anon, 1992, 1994). Despite these efforts only a fraction – 4.1% – of the forest land has been

protected (Anon., 2002). Small areas cannot generally sustain high species numbers (Connor & McCoy, 1979; MacArthur & Wilson, 1967). Further, the isolation of the protected areas may increase the risk for a local extinction (Andrén, 1997; Hanski, 1998), even if the habitats were suitable for a species (see also Kouki & Väänänen, 2000).

Conservation efforts are further complicated by the fact that many threatened species do not necessarily depend on the forest age (or old-growth) as such but rather on some specific habitat characteristic that may or may not occur within an old-growth area (Kouki, Löfman, Martikainen, Rouvinen, & Uotila, 2001). Such local habitat properties include, for example, coarse woody debris (CWD), dead wood, charred wood, or specific host tree species. Since boreal forest ecosystems are characterised by successional changes, the local habitat properties will keep changing even in the absence of any human influence: the conservation value of an area does not depend only on its current ecological characteristics but also on how these characteristics will change in the future.

One of the most important micro-habitat for several threatened species in the conifer-dominated old-growth boreal forests is the European aspen (*Populus tremula* L.) (e.g. Esseen et al., 1997). Large-diameter aspens typically occur as scattered individuals or tree groups within natural old-growth boreal forests (Syrjänen, Kalliola, Puolasmaa, & Mattsson, 1994). Their regeneration is facilitated by both large scale fires and windstorms but also through small-scale gap dynamics that create openings suitable for aspen regeneration (Peterson & Squiers, 1995; Syrjänen et al., 1994; Tikka, 1954). Since aspen is the intermediate host for the pine rust fungus (*Melampsora pinitorqua* Braun (Rostr.)) (Kurkela, 1973), the species has been systematically eliminated from the managed forests in Finland. For example, the recent national forest inventory (2000) revealed an average living aspen volume of 1.1 m³/ha and dead volume of only 0.1 m³/ha in the current study region (Korhonen et al., 2001), and similar aspen volumes have been reported from other parts of Fennoscandia, too (e.g. Fridman & Walheim, 2000).

Large aspen trees host hundreds of both herbivorous and saproxylic invertebrates, polypore fungi and epiphytic lichens and roughly 150 of these are specialists, occurring only on or in aspen trees (Table 1). Also some vertebrates, such as woodpeckers (Angelstam & Mikusinski, 1994) and the flying squirrel (Reunanen, Mönkkönen, & Nikula, 2000), are at least partly dependent on the aspen. Aspen leaf litter creates preferred habitat for

Table 1. Number of species in some taxonomic groups associated with the European aspen (*Populus tremula* L.) in Finland

Group	No. of species	No. of specialists	No. of threatened species
Herbivorous			
macrolepidoptera	112	14	0
Beetles	40	16	0
Sawflies	30	12	0
Saproxylic beetles	300+	35–45	31+
Polypore fungi	60	10	5
Epiphytic lichens	200	40	8
Molluscs	–	–	3

The table is based mostly on compilation data collected by Siitonen (1999), with some additions from Anon (2000) and Rassi et al. (2001). In addition to the groups shown, aspen-associated species are found also among other taxonomic groups (diptera, bryophytes, vertebrates, mycorrhizal fungi) but the knowledge on these is too limited or their classification is unclear to be included in the table. – = no data available, + = a likely underestimate.

several ground-dwelling invertebrates, probably because the litter is less acid than the typical needle litter in the boreal forests (Koivula, Punttila, Haila, & Niemelä, 1999).

A large proportion of aspen-associated species are specialists on dead aspens and about 50 of these species are currently threatened in Finland (Rassi et al., 2001; Siitonen, 1999; Siitonen & Martikainen, 1994). Aspen has even been designated as a focal micro-habitat in terms of biodiversity protection in the Fennoscandian area (see, e.g. Esseen et al., 1997).

When an aspen tree dies it goes through a characteristic decay process, beginning from a partly dead, perhaps a hollow standing tree to lying dead tree, and eventually decomposes after some decades (Tikka, 1954, 1956). Each decay class is characterised by specific beetle and fungus species, a pattern similar to other boreal tree species (Ehnström, 2001; Ehnström & Waldén, 1986; Jonsell, Weslien, & Ehnström, 1998; Palm, 1959; Samuelsson, Gustafsson, & Ingelög, 1994). To sustain local survival of the species, each decay class should be continuously available within a protected forest or within the dispersal distance of the species (Jonsell, Nordlander, & Jonsson, 1999). In a small area with low aspen density bottlenecks with no availability of the specific decay class may occur and this could lead to local extinction of species that depend on the specific decay class.

We will address the problems of the quality and dynamics of conservation areas based on empirical data on the micro-habitat occurrence within a network of old-growth protected areas. This study has three aims:

1. to assess the present structure of aspen populations within the network of protected old-growth forests;

2. to assess the current value – in terms of dead wood amount and variability – of protected old-growth forests to aspen-associated species; and
3. to evaluate if the forest reserve network will facilitate long-term survival of the aspen-associated species.

Methods

Study areas and the reserve network

Our study region is located in North Karelia, eastern Finland (63°20'N, 30°30'E). The forests in the area are dominated by pine (*Pinus sylvestris* L.) and spruce (*Picea abies* (L.) Karsten), with birch (*Betula* spp.) less abundant, and other species – such as aspen, rowan (*Sorbus aucuparia* L.) and alder (*Alnus incana* (L.) Moench) – occurring patchily within the area.

A few national parks were established in North Karelia during 1970s and 1980s but the protection programme specifically aimed at old-growth forest protection was launched in 1990s (Anon, 1992, 1994). In the whole North Karelia there are 74 old-growth protection areas, covering 4989 ha (the total forest land area in North Karelia is 1 369 000 ha) (Anon, 1992, 1994). In addition, the six national parks (covering ca. 30 000 ha) also include some old-growth areas in addition to lakes and peatlands. About 95% of the forests in the study region are currently intensively managed for timber production (Korhonen et al., 2001) and their structural characteristics differ from the natural forests (Löfman & Kouki, 2001; Siitonen, Martikainen, Punttila, & Rauh, 2000; Uotila et al., 2002; Uotila, Maltamo, Uuttera, & Isomäki, 2001).

The protected areas are not virgin, natural boreal forests, but rather show a varying degree of past human activity (Aarnio, 1999; Lehtonen & Huttunen, 1997; Pitkänen & Huttunen, 1999). Thus, the protected areas are better regarded as semi-natural rather than natural boreal forests.

The areas included in the programme were selected on the basis of their resemblance to the natural forests as revealed by field inventories. Occurrence of the old aspen and other deciduous trees was one of the criteria when the protected areas were selected (Anon., 1992) but the field inventories were rapidly done with only rough assessment of the characteristics.

For this study we randomly selected 15 protected areas for a detailed analysis of aspen occurrence. The study areas were selected so that the driest pine-dominated forests were excluded, since aspens in these areas are also naturally rare (Esseen et al., 1997). The size of the studied protected areas varied between 14.8 and 401.2 ha. The total area covered by the field inventories was 1570 ha, i.e. 31% of the areas included in the protection programme. The study areas and their basic characteristics are shown in Table 2.

Field inventories

From each area we counted all aspen trees by slowly walking through each area so that the whole forest was efficiently covered. The total number of trees included in the data is 32 903 trees. Each area was carefully checked so that no single aspen tree or sapling was left unnoticed. Approximately 2 ha were covered in 1 h and the field work was done by the author KA. The protected areas were completely covered except in Vankonvaara. Due to time limitations only a portion of the Vankonvaara forest could be covered (26.7 ha of the 53 ha protected area), but we have included also these data into the analysis. The inventories were done between 23 June and 10 September 1999.

Although all the aspens were counted, more detailed ecological characteristics were measured only from the larger trees. The size limit for measuring detailed tree characteristics was 5 cm diameter at breast height (dbh). Trees smaller than this size were counted, classified as saplings but no further measurements were taken. Most of the measurements done are not easily taken from or are not informative for the smallest trees.

The following characteristics were measured for each tree of at least 5 cm dbh. First the tree was classified as dead or living. The height of the tree was estimated visually with calibration measures

Table 2. Studied protected areas, their sizes and basic characteristics of the aspen populations (dbh = diameter at breast height)

Name of the area	Area (ha)	No. of saplings dbh < 5 cm per site	No. of trees dbh ≥ 5 cm per site	No. of living trees per site	No. of dead trees per site	Volume (m ³) of living trees per ha	Volume (m ³) of dead trees per ha
Heinävaara	100.9	303	578	85	493	0.46	1.26
Honkavaara	21.9	1236	226	110	116	2.48	1.69
Jäkäläkangas	223.8	336	1747	126	1621	0.31	2.02
Jyrinvaara	118.2	1295	655	274	381	1.78	0.86
Massivaara	37.2	2040	713	398	315	5.05	1.73
Oinasvaara	20.7	528	288	87	201	2.85	3.83
Pahavaara	28.6	3002	565	329	236	6.91	1.93
Pahkavaara	100.4	342	608	74	534	0.46	1.89
Pieni Hovinvaara	19.3	548	704	153	551	3.79	6.93
Pönttövaara	288.7	651	1327	119	1208	0.19	1.07
Putkisenvaara	401.2	3268	2724	1105	1619	1.51	1.14
Ruunavaara	38.2	867	1033	82	951	1.15	8.03
Sini-Körtelinvaara	129.6	2544	2111	1348	763	5.74	1.30
Simivaara	14.8	1576	230	135	95	5.00	1.66
Vankonvaara	26.7	309	549	77	472	2.65	6.30
Total	1570.2	18845	14058	4502	9556		

taken occasionally. The dead trees were further classified as standing and lying. If the tree was a whole tree, its dbh was taken similarly as for the living trees. If the dead tree was just a part of the stem we measured its length and dbh from both ends of the stem.

Decay class of each trunk was assessed using a knife and measuring how deep into the wood it can be easily pushed. The method is comparable to those used in several Fennoscandian studies that have assessed the tree decay (see Siitonen et al., 2000 and references therein). The following categories were used for standing and lying dead trees:

A knife is easily pushed:

1 = 0 cm (for standing) or few mm (for lying)

2 = 1–2 cm

3 = 3–5 cm

4 = knife goes in completely

5 = falling into pieces (only for lying trees).

Any marks of tree notching and girdling were also recorded. Notching was widely applied as a part of silvicultural activities during 1960–1980. The purpose was to remove the economically useless aspen from the managed forests. Killing aspens with notching is more effective way to remove aspen from a forest because this reduces also root sprouting better than, for example, logging the tree.

We took core samples of over 200 trees for the age determination, but these were not used in further analyses. The core samples taken from aspen trees are usually very difficult to date, as many of the larger trees are already rotting from inside. Tikka (1956) observed that by the age of 60 years most aspen stems (80%) are already at least partly decayed. Thus, the tree ring counting is often not possible, especially of the bigger trees. Instead of core samples we used dbh measurements to describe the age structure of the aspen population. According to Tikka (1954) the correlation between aspen age and dbh is almost linear in mixed forests. Linear correlation between age and size was observed by Ripple and Larsen (2000) also for the North American trembling aspen (*Populus tremuloides* Michx.).

Calculations

The volume of the trees was calculated using the volume equations of Laasasenaho (1982) that are based on regression formulas using dbh and height of the tree. Laasasenaho (1982) does not provide equations for aspen, and we used the equations for birch instead. As both species are deciduous this should not introduce considerable errors. The

absolute volume estimations may be slightly and systematically biased but we should still be able to reliably assess the relative proportion of tree volumes between areas and decay classes, for example.

The equations by Laasasenaho (1982) were used for living trees and unbroken dead trees. For broken dead stems (standing and lying) and snags we applied the formula for a cylinder calculated on the basis of mid-diameter and height or length of the tree.

Both the aspen density (number of trees per ha, volume per ha) and the absolute amount of aspen trees in a protected area (number of trees per area, volume per area) are important for associated species. The former gives indication of the local density of the habitat available while the latter can be used to assess the overall importance of single area in the network of the conservation areas.

Results

Aspen densities, volumes and microhabitat diversity

Both the absolute number (trees per area) and densities (volume per ha) showed highly variable pattern in different areas (Fig. 1, Table 2). The number of living trees (dbh > 5 cm) varied between 74 and 1347 in different areas. The volumes were between 0.19 and 6.91 m³/ha for the living trees and 0.86 and 8.03 m³/ha for dead trees. The

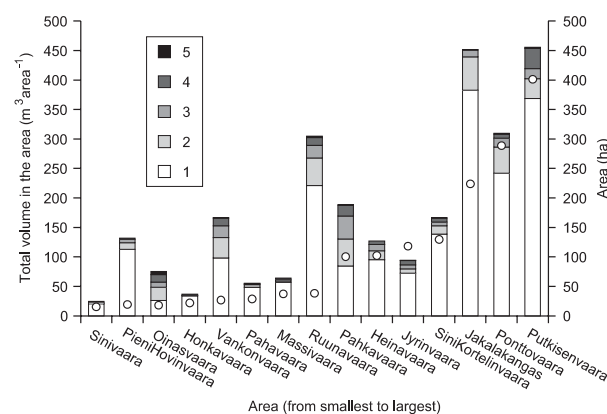


Figure 1. Total dead tree volume (including both standing and lying dead trees) and the availability of different decay classes (1–5, see Field inventories for the explanation of the classes) in the protected areas. Areas are ordered from the smallest (left) to the largest on the x-axis. Size of the area is shown by an open circle, with corresponding axis on the right.

number of saplings (dbh < 5 cm) varied between 303 and 3268 trees per area, clearly exceeding the number of living trees bigger than 5 cm dbh. There were also differences in the volumes of different decay classes indicating qualitative differences between the areas in the current aspen availability (Fig. 1).

The high amount of the decay class 1 (= recently died) is notable. The notching of aspens was widely and intensively practised in the conservation areas before they were established as set-asides. The activity peaked during the 1970s and 1980s. The proportion of notched trees among all the dead trees accounted about half of the total dead volume in some sites (Fig. 2). A more detailed and a typical example is given in Fig. 3 for Heinävaara. As notching causes a tree to die and dry rapidly, it initially promotes the amount of trees belonging to the first decay class. Thus, the high proportion of decay class 1 in the areas is largely caused by the previous human activities. Although some of trees that were notched might have died naturally anyway, the notching has apparently caused a pulse-like increase in dead volume availability in the conservation areas.

Size of the area and aspen availability: are large areas also qualitatively the best?

In terms of tree densities (volume per ha, no. per ha) the smallest areas contained highest aspen densities (correlation between size of the area and the density of saplings was $r_s = -0.79$, $p < 0.001$,

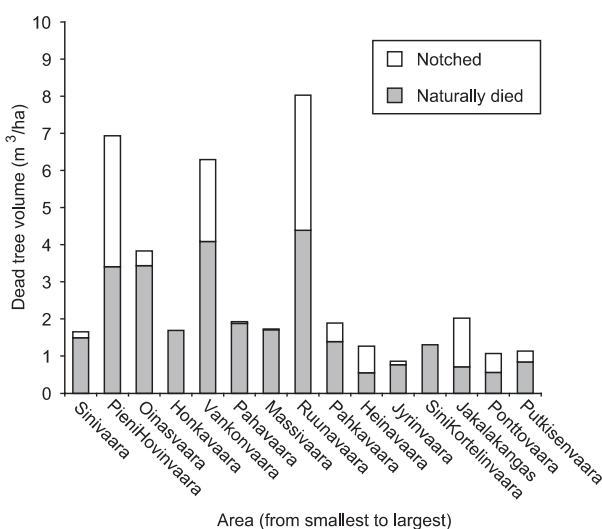


Figure 2. The proportion of naturally died and notched trees of the total dead wood volume. In many areas, about half of the dead tree volume is formed by notched trees.

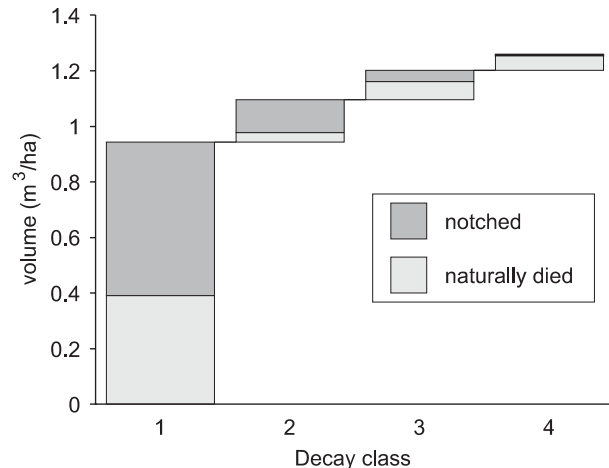


Figure 3. The cumulative structure of dead volume ($1.26 \text{ m}^3/\text{ha}$) of dead aspens in Heinävaara. Note the large contribution of notched trees to the dead volume in decay classes 1 and 2. Decay classes shown from the least decayed (1) to highly decayed (4; see Field inventories for the description of the classification used).

between size and living tree volume $r_s = -0.56$, $p = 0.030$, and between size and dead tree volume $r_s = -0.55$, $p = 0.035$). The negative correlation was thus especially clear among the saplings that occurred with very low densities in the larger areas and were most abundant near the reserve edges where gap dynamics (for example, due to wind-thrown trees) are characteristic.

The absolute amount of the dead aspens, however, showed positive relationship with the area (Fig. 1). Largest areas (such as Jäkäläkangas and Putkisenvaara) contained the largest amounts of dead aspens, but also some smaller areas (Pieni Hovinvaara, Vankonvaara and Ruunavaara) stood out with high aspen availability.

The diversity of different decay classes was not clearly related to the size of the area (Fig. 1). For example, Jäkäläkangas had very high total amount of dead aspens, but with low availability of decay classes 4 and 5. Oinasvaara, an example of small area, had high decay class diversity with for example, better availability of decay class 4 than in Jäkäläkangas.

Size structure of aspens and predicted dynamics

The size distribution of both dead and living trees peaked at the dbh class of 20–30 cm (Fig. 4). Thus, almost all the areas are dominated by middle-aged trees. A large proportion of the dead aspens at the size classes 20–30 cm were killed by the notching.

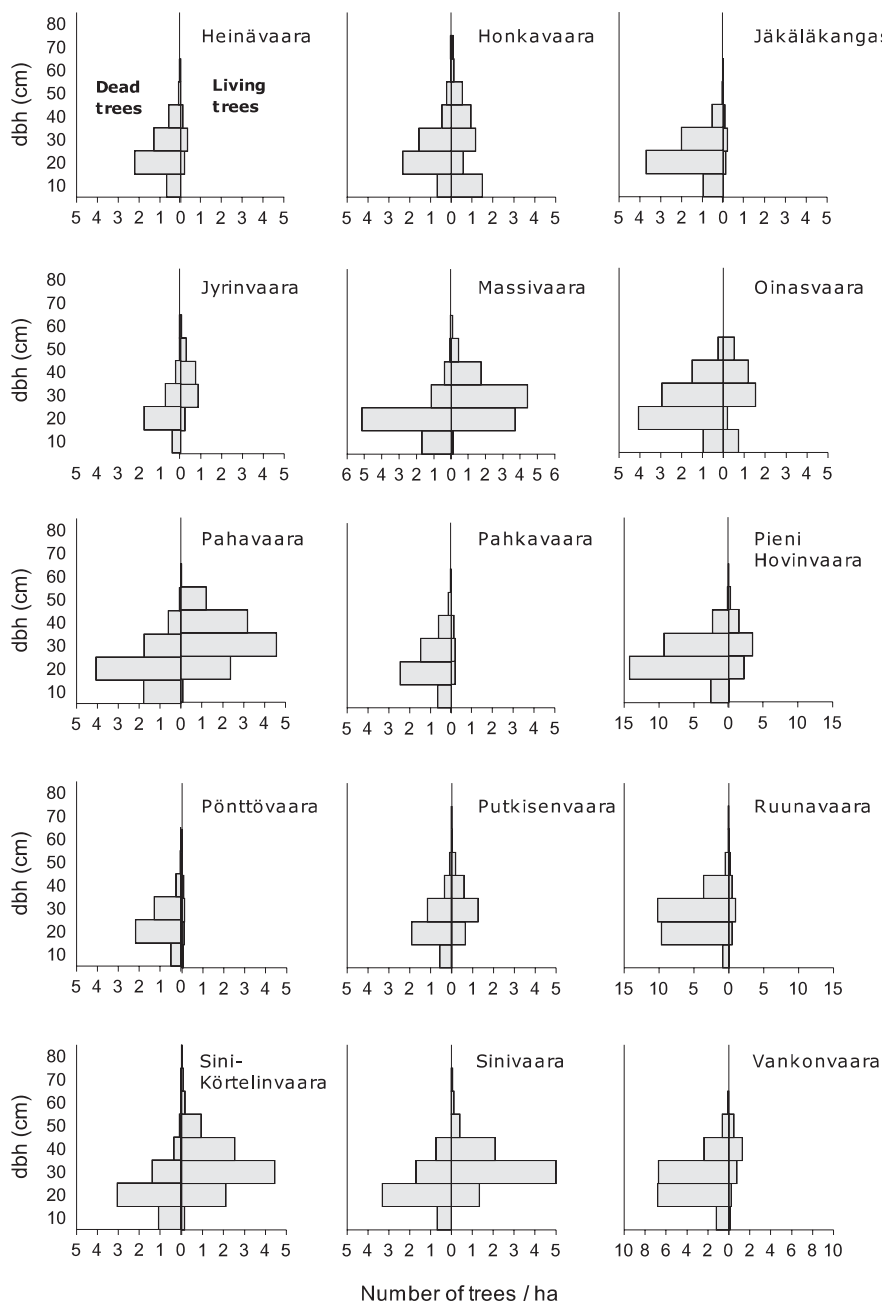


Figure 4. Size distribution of dead (left) and living (right) aspens in the 15 study areas. The distributions are based on classified data. Y-axis values are classified as follows 10 equals $5 \text{ cm} \leq \text{dbh} < 15 \text{ cm}$, 20 equals $15 \text{ cm} \leq \text{dbh} < 25 \text{ cm}$ and so on. Note that young trees ($5 \text{ cm} \leq \text{dbh} < 25 \text{ cm}$) are relatively rare in many areas, showing the emerging bottleneck for the aspen-associated species. Saplings ($\text{dbh} < 5 \text{ cm}$) are omitted from the figures, but shown in Table 2.

Several of the areas have very low density of living aspens. For example, Heinävaara, Jäkäläkangas and Pönttövaara had aspen densities well below one tree per hectare. Thus, availability of the aspens is highly fragmented also within the protected areas. Only four areas (Massivaara, Pahavaara, Sini-Körtelinvaara and Sinivaara) out of 15 showed higher occurrence of the living aspens in different dbh classes (Fig. 4).

There was an almost total absence of young trees in the size 5–15 cm. This applies to all the areas except Honkavaara and Oinasvaara. However, the young saplings ($\text{dbh} < 5 \text{ cm}$) were rather abundant in all the areas (Table 2).

In the long run the size distribution with no new tree cohort emerging means that aspens will eventually disappear from the area. Being rather fast-growing tree the middle-sized aspens currently

abundant will reach their maturity and death probably within the next 20–40 years (for growth, see Tikka, 1954).

Discussion

Quality of the protected area network for aspen-associates

Several theoretical studies have emphasised that regional population dynamics cannot be analysed without addressing the colonisation–extinction dynamics at the metapopulation level (e.g. Hanski, 1998; Hanski & Gilpin, 1991; Hasting & Harrison, 1994; Tilman & Kareiva, 1997). Even though these approaches have provided us with new ideas on how to protect the species in fragmented and patchy habitats, the modelling work has still some shortcomings when applied to real landscapes (Hanski, 1999). For example, only rarely have the local habitat characteristics within the patch network of conservation areas have been assessed and their dynamics evaluated (Harrison & Bruna, 1999; Stelter et al., 1997; Thomas, 1994). Obviously, understanding and predicting the functioning of a reserve network requires that detailed attention is paid to the specific habitat that a species depends on and also on dynamic aspects that affect these micro-habitats (see also Johst et al., 2002; Keymer et al., 2000).

Our study aimed at analysing the availability and dynamics of one specific habitat characteristic – aspen trees – that occurs within the protected areas. Because about 50 species of the 233 threatened old-growth species in Finland are dependent on these aspen trees (Table 1), the results are highly relevant when assessing the structural and functional properties of the old-growth conservation area network.

This study of the occurrence of the specific habitat property reveals quite different patterns than can be simply deduced from – for example – aerial coverage of the old-growth. Although there is a relationship between aspen availability and size of the protected area (Fig. 1), the size is not always directly related to the availability of this specific habitat (aspen). This emphasises the fact that local qualities of the protected areas must be taken into account when designing a network and when assessing its functioning. If small areas have high substrate availability, their “effective size” in terms of species protection is higher than can be judged from their actual extent.

Overall, the current results of both the living and dead aspen trees, their amounts and qualities show that the protected areas are qualitatively highly variable for protecting the aspen-associated species.

Dynamic bottlenecks mediated through external factors

The current size distribution of dead and living trees within the protected areas suggests that major qualitative and quantitative changes in aspen availability are expected even though the areas are currently protected. Recruitment of aspen to the canopy is very poor in all the study areas despite the high sapling densities. Unless this is caused by a recent burst of regeneration it suggests that young trees (dbh 5–15 cm) cannot survive beyond the sapling phase probably because of browsing pressure of mammalian herbivores (Angelstam, 1996; Angelstam, Wikberg, Danilov, Faber, & Nygrén, 2000; Cederlund & Bergström, 1996; McInnes, Naiman, Pastor, & Cohen, 1992; Risenhoover & Maass, 1987).

Aspen is preferred food for hares and especially for moose (*Alces alces*) (e.g. Jalkanen, 2001). The moose population has rapidly increased in Finland during the past 50 years (Fig. 5). The population explosion is caused mostly by changes in the hunting policy (Nygrén, 1996; Nygrén & Pesonen, 1993), but also by the lack of large carnivorous species – such as wolves – both in our study region and in the whole of Finland, a pattern similar to what Ripple and Larsen (2000) and Ripple, Larsen, Renkin, and Smith (2001) reported

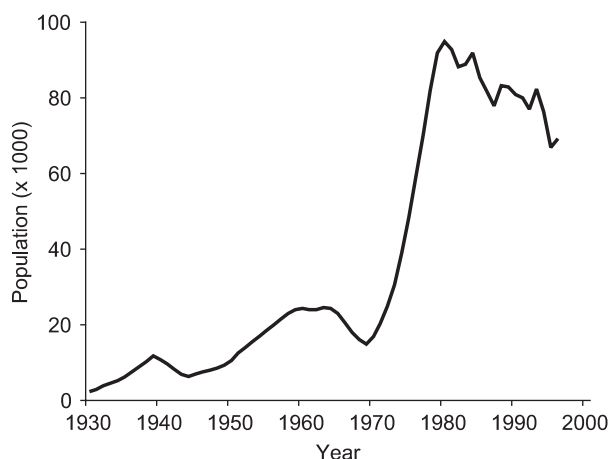


Figure 5. Moose population in Finland between 1930 and 1995, based on winter population censuses (data from Nygrén, 1996 and presented here with the permission of Tuire Nygrén and Mauri Pesonen).

from the Yellowstone area. For example, comparison of current moose densities between Finnish North Karelia and adjacent Russian Karelia shows a 2–4-fold difference (Helle, Wikman, Danilov, Bljudnik, & Belkin, 2000). In the Russian Karelia wolves, on the other hand, are 4–5 times more abundant based on the recent game censuses.

The ecosystem effects of moose browsing are substantial (Bailey & Whitham, 2002; McInnes et al., 1992; Risenhoover & Maass, 1987). The impact of browsing specifically on the conservation areas has not been thoroughly studied, but studies elsewhere suggest high potential impacts (Kay, 1997; Ripple & Larsen, 2000; Romme, Turner, Wallace, & Walker, 1995). The protected areas are thus profoundly influenced by the factors originating from outside the area (Janzen, 1983; Väisänen, Järvinen, & Rauhala, 1986).

The predicted dynamics within the protected areas cast serious doubts to long-term functioning of the reserve network (see also Kay, 1997; Ripple & Larsen, 2000; Romme et al., 1995). If aspen disappears from the areas, all the species that specialise on aspen will also disappear. A similar pattern holds for the whole conservation network, not just to individual protected areas (Fig. 4). In the long-run the network is predicted to change to quite unsuitable habitat for many of the species that it was originally set up to protect.

Conclusions and management implications

The dynamics of spatially divided populations have been studied in depth during the past years. These modelling exercises have provided useful ideas and tools also for conservation biology. The messages that emerge are not encouraging for species protection. For example, Hanski (2000) recently pointed that if the species protection is based on the current conservation network, even up to 1000 species from the Finnish old-growth may disappear within the next decades and centuries.

Our study highlights the importance of habitat quality within the protected old-growth network. Many of the aspen-associated species are likely to disappear simply because of the projected habitat changes. Thus, the reasons for regional extinction for the aspen-associated species are not due to the stochastic colonisation–extinction dynamics that are often assumed in the spatial population models (Hanski, 1998, 1999), but rather from purely deterministic processes related to habitat degradation in the patches. A similar pattern was observed by Stelter et al. (1997) in another case study where the habitat is prone to disturbance and succession.

Such quality changes may be more common than has been assumed (Harrison & Bruna, 1999).

The predicted habitat change in the old-growth patches and its consequences are important for two more reasons: it will likely happen quite fast because aspen is relatively fast-growing and rapidly decaying species (e.g. Tikka, 1954, 1956), and it will happen in almost every area. Because the regeneration of the aspen is hindered in practically all the areas (Fig. 4), the associated species cannot survive regionally by colonising other protected areas.

The emerging conservation problem can be alleviated in several different ways. First, protected areas are – by definition – not currently managed in any way. If the aspen would benefit from management actions that would mimic natural disturbances (such as fire or creation of small gaps) then implementing some management actions might be considered also in the protected areas. This was also proposed for forest reserves in northern Sweden by Linder, Elfving, and Zackrisson (1997). Lack of natural disturbances in the protected areas may considerably change the tree composition towards spruce-dominance. However, as the protected areas cover only a fraction in Finland, these activities should rather be implemented in the adjacent managed forests.

Second, the reduction of the size of the moose population would likely help in promoting successful aspen regeneration.

Third, aspen should be promoted in the surrounding managed forests, e.g. by leaving all the few scattered large aspens as retention trees and promoting aspen regeneration in clear-cut areas.

Although it is unlikely that all the aspen-associated species can survive in the trees located in sunny clear-cut openings, many of them can (Jonsell et al., 1998; Martikainen, 2001; Martikainen, Penttilä, Kotiranta, & Miettinen, 2000; Palm, 1959; Sverdrup-Thygeson & Ims, 2002). For example, Martikainen (2001) compared the species composition of the threatened species in aspen trees located in the middle of old-growth and in the middle of clear-cuts. The majority of the species were able to survive on (or they even seem to prefer) aspen trees located in clear-cuts. Kolström and Lumatjärvi (2000) have modelled aspen dynamics in commercial forests and their results show that this kind of tree retention can be highly beneficial for the aspen-associated species. Thus, successful protection of the several aspen-associated threatened species can be enhanced both in the protected areas and the surrounding managed forests. Relying only on the currently protected areas will not probably save these species in the

long run. Inevitable habitat changes in the protected areas will likely lead to impoverishment of the populations of the aspen-associated species.

Acknowledgements

Kaija Eisto (Finnish Forest and Park Service) helped in selecting the study areas and gathering tools (such as aerial photos) needed in the field work. Kari T. Korhonen provided us with some additional aspen data from the National Forest Inventory (NFI) database of the Finnish Forest Research Institute. Discussions with Per Angelstam and Heikki Kotiranta helped in formulating the manuscript. The manuscript was commented and improved by Bengt Gunnar Jonsson, Lars Edenius, Juha Siitonen and Maarit Similä. Comments made by anonymous referee were especially useful. This study was funded by the Finnish Forest and Park Service (Metsähallitus) and the Academy of Finland (Finnish Centre of Excellence Programme 2000–2005, project no. 64308).

References

- Aarnio, J. (1999). Kaskiviljelystä metsätöihin. Tutkimus Pielisjärven kruunumetsistä ja kruununmetsätorppareista vuoteen 1910 (From slash-and-burn cultivation to forest work: research on the crown forests of the municipality of Pielisjärvi and tenant farmers on crown forest land up until 1910; in Finnish with English summary). Ph. D. Thesis, University of Joensuu.
- Andrén, H. (1997). Habitat fragmentation and changes in biodiversity. *Ecological Bulletins*, *46*, 171–181.
- Angelstam, P. (1996). The ghost of forest past – natural disturbance regimes as a basis for reconstruction of biologically diverse forest in Europe. In R. M. DeGraaf, & R. I. Miller (Eds.), *Conservation of faunal diversity in forested landscapes* (pp. 287–337). London: Chapman & Hall.
- Angelstam, P., & Mikusinski, G. (1994). Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. *Annales Zoologici Fennici*, *31*, 157–172.
- Angelstam, P., Wikberg, P.-E., Danilov, P., Faber, W. E., & Nygrén, K. (2000). Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. *Alces*, *36*, 133–145.
- Anon. (1992). Vanhojen metsien suojelu valtion mailla etelä-Suomessa (Protection programme for old-growth forests in southern Finland), Rep. No. 70/1992. Ympäristäministeriö – Ministry of Environment, Helsinki.
- Anon. (1994). Vanhojen metsien suojeluohjelman täydennys Etelä-Suomessa (Protection programme for old-growth forests in southern Finland, additions), Rep. No. 2/1994. Ympäristöministeriö – Ministry of Environment, Helsinki.
- Anon. (2000). Metsien suojelun tarve Etelä-Suomessa ja Pohjanmaalla. Etelä-Suomen ja Pohjanmaan metsien suojelun tarve-työryhmän mietintö (Forest protection in southern Finland and Ostrobothnia). Suomen ympäristö no., 437, pp. 1–284.
- Anon. (2002). Metsien suojelun luokittelun ja tilastoinnin yhtenäistämistyöryhmä, Rep. No. 2002:15 (ISSN 0781-6723). Maa ja metsätalousministeriö – Ministry of Agriculture and Forestry, Helsinki.
- Bailey, J. K., & Whitham, T. G. (2002). Interactions among fire, aspen, and elk affect insect diversity: Reversal of a community response. *Ecology*, *83*, 1701–1712.
- Bonan, G. B., & Shugart, H. H. (1989). Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, *20*, 1–28.
- Borman, F. H., & Likens, G. E. (1979). Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist*, *67*, 660–669.
- Cederlund, G., & Bergström, R. (1996). Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. In R. M. DeGraaf, & R. I. Miller (Eds.), *Conservation of faunal diversity in forested landscapes* (pp. 265–281). London: Chapman & Hall.
- Connor, F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *American Naturalist*, *113*, 791–833.
- Ehnström, B. (2001). Leaving dead wood for insects in boreal forests – Suggestions for the future. *Scandinavian Journal of Forest Research*, *3*(Suppl.), 91–98.
- Ehnström, B., & Waldén, H. W. (1986). Faunavård i skogsbruket. Del 2. Den lägre faunan Skogsstyrelsen, Jönköping.
- Esseen, P.-A., Ehnström, B., Ericson, L., & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins*, *46*, 16–47.
- Fridman, J., & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, *131*, 23–36.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49.
- Hanski, I. (1999). Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, *87*, 209–219.
- Hanski, I. (2000). Extinction debt and species credit in boreal forests: Modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici*, *37*, 271–280.
- Hanski, I., & Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of Linnean Society*, *42*, 3–16.
- Harrison, S. (1994). Metapopulations and conservation. In P. J. Edwards, R. M. May, & N. R. Webb (Eds.), *Large-scale ecology and conservation biology* (pp. 111–128). Oxford: Blackwell.
- Harrison, S., & Bruna, E. (1999). Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography*, *22*, 225–232.

- Hasting, A., & Harrison, S. (1994). Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, 25, 167–188.
- Helle, P., Wikman, M., Danilov, P., Bljudnik, L., & Belkin, V. (2000). Riistalaskennat talvella 2000 Suomessa ja Venäjän Karjalassa. *Riistantutkimuksen Tiedote (Reports of the Finnish Game Research Institute)*, 169, 1–16.
- Hofgaard, A. (1993). 50 Years of change in a Swedish boreal old-growth *Picea abies* forest. *Journal of Vegetation Science*, 4, 773–782.
- Jalkanen, A. (2001). The probability of moose damage at the stand level in southern Finland. *Silva Fennica*, 35, 159–168.
- Janzen, D. H. (1983). No park is an island: Increase in interference from outside as park size decreases. *Oikos*, 41, 401–410.
- Johst, K., Brandl, R., & Eber, S. (2002). Metapopulation persistence in dynamic landscapes: The role of dispersal distance. *Oikos*, 98, 263–270.
- Jonsell, M., Nordlander, G., & Jonsson, M. (1999). Colonization patterns of insects breeding in wood-decaying fungi. *Journal of Insect Conservation*, 3, 145–161.
- Jonsell, M., Weslien, J., & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, 7, 749–764.
- Kay, C. E. (1997). The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for ecological integrity. *Canadian Field-Naturalist*, 4, 607–616.
- Keymer, J. E., Marquet, P. A., Velasco-Hernandez, J. X., & Levin, S. A. (2000). Extinction thresholds and metapopulation persistence in dynamic landscapes. *American Naturalist*, 156, 478–494.
- Koivula, M., Punttila, P., Haila, Y., & Niemelä, J. (1999). Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forests. *Ecography*, 22, 424–435.
- Kolström, M., & Lumatjärvi, J. (2000). Saproxylic beetles on aspen in commercial forests: A simulation approach to species richness. *Forest Ecology and Management*, 126, 113–120.
- Korhonen, K. T., Tomppo, E., Henttonen, H., Ihalainen, A., Tontteri, T., & Tuomainen, T. (2001). Pohjois-Karjalan metsäkeskuksen alueen metsävarat 1996–2000. *Metsätieteen Aikakauskirja*, 3B/2001, 495–576.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., & Uotila, A. (2001). Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research*, 3(Suppl.), 27–37.
- Kouki, J., & Väänänen, A. (2000). Impoverishment of resident old-growth forest bird assemblages along isolation gradient of protected areas in eastern Finland. *Ornis Fennica*, 77, 145–154.
- Kurkela, T. (1973). Epiphytology of *Melampsora* rusts of Scots pine (*Pinus sylvestris* L.) and aspen *Populus tremula* L. *Metsäntutkimuslaitoksen Tiedonantoja*, 79, 1–68.
- Laasasenaho, J. (1982). Taper-curve and volume functions for pine, spruce and birch. *Communications Institutii Forestalis Fenniae*, 108, 1–74.
- Lehtonen, H., & Huttunen, P. (1997). History of forest fires in eastern Finland from the fifteenth century AD – the possible effects of slash-and-burn cultivation. *The Holocene*, 7, 223–228.
- Linder, P., Elfving, B., & Zackrisson, O. (1997). Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, 98, 17–33.
- Löfman, S., & Kouki, J. (2001). Fifty years of landscape transformation in managed forests of southern Finland. *Scandinavian Journal of Forest Research*, 16, 44–53.
- Maarel, E. van der. (1993). Some remarks on disturbance and its relation to diversity and stability. *Journal of Vegetation Science*, 4, 733–736.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. New Jersey: Princeton University Press.
- Martikainen, P. (2001). Conservation of threatened saproxylic beetles: Significance of retained aspen *populus tremula* on clearcut areas. *Ecological Bulletins*, 49, 205–218.
- Martikainen, P., Penttilä, R., Kotiranta, H., & Miettinen, O. (2000). New records of *Funalia trogii*, *Perenniporia tenuis* and *Polyporus pseudobetulinus* in Finland, with notes on their habitat requirements. *Karstenia*, 40, 79–92.
- McInnes, P. F., Naiman, R. J., Pastor, J., & Cohen, Y. (1992). Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, 73, 2059–2075.
- Niklasson, M., & Granström, A. (2000). Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, 81, 1484–1499.
- Nygrén, T. (1996). Hirvi (*Alces alces*). In H. Lindén, M. Hario, & M. Wikman (Eds.), *Riistan jäljille* (pp. 103–108). Helsinki: Edita.
- Nygrén, T., & Pesonen, M. (1993). The moose population (*Alces alces* L.) and methods of moose management in Finland, 1975–89. *Finnish Game Research*, 48, 46–53.
- Paine, R. T., & Levin, S. A. (1981). Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs*, 51, 145–178.
- Palm, T. (1959). Die Holz- und Rinden-Käfer der süd- und mittelschwedischen Laubbäume. *Opuscula Entomologica Supplementum*, 16, 1–374.
- Peterson, C. J., & Squiers, E. R. (1995). Competition and succession in an aspen-white-pine forest. *Journal of Ecology*, 83, 449–457.
- Pitkänen, A., & Huttunen, P. (1999). A 1300-year forest-fire history at a site in eastern Finland based on charcoal and pollen records in laminated lake sediment. *The Holocene*, 9, 311–320.
- Rassi, P., Alanen, A., Kanerva, T., & Mannerkoski, I. (Eds.) (2001). *Suomen lajien uhanalaisuus 2000 Threatened*

- species in Finland in 2000*. Helsinki: Ympäristöministeriö & Suomen Ympäristökeskus.
- Remmert, H. (1991). *The mosaic-cycle concept of ecosystems*. Berlin: Springer.
- Reunanen, P., Mönkkönen, M., & Nikula, A. (2000). Managing boreal forest landscapes for flying squirrels. *Conservation Biology*, 14, 218–226.
- Ripple, W. J., & Larsen, E. J. (2000). Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation*, 95, 361–370.
- Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, 102, 227–234.
- Risenhoover, K. L., & Maass, S. A. (1987). The influence of moose on composition and structure of Isle Royale forest. *Canadian Journal of Forest Research*, 17, 357–364.
- Romme, W. H., Turner, M. G., Wallace, L. L., & Walker, J. S. (1995). Aspen, elk, and fire in northern Yellowstone National Park. *Ecology*, 76, 2097–2106.
- Samuelsson, J., Gustafsson, L., & Ingelög, T. (1994). Dying and dead trees – a review of their importance for biodiversity Swedish Threatened Species Unit, Swedish Environmental Protection Agency, Uppsala.
- Siitonen, J. (1999). Haavan merkitys metsäluonnon monimuotoisuudelle. In J. Hynynen, & A. Viherä-Aarnio (Eds.), *Haapa – monimuotoisuutta metsään ja metsätalouteen – Metsäntutkimuslaitoksen tiedonantoja 725* (pp. 71–82). Vantaa: Metsäntutkimuslaitos.
- Siitonen, J., & Martikainen, P. (1994). Occurrence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research*, 9, 185–191.
- Siitonen, J., Martikainen, P., Punttila, P., & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management*, 128, 211–225.
- Stelter, C., Reich, M., Grimm, V., & Wissel, C. (1997). Modelling persistence in dynamic landscapes: Lessons from a metapopulation of the grasshopper bryodemata tuberculata. *Journal of Animal Ecology*, 66, 508–518.
- Sverdrup-Thygeson, A., & Ims, R. A. (2002). The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation*, 106, 347–357.
- Syrjänen, K., Kalliola, R., Puolasmaa, A., & Mattsson, J. (1994). Landscape structure and forest dynamics in subcontinental Russian European taiga. *Annales Zoologici Fennici*, 31, 19–34.
- Thomas, C. D. (1994). Extinction, colonization, and metapopulations: Environmental tracking by rare species. *Conservation Biology*, 8, 373–378.
- Thomas, C. D., & Hanski, I. (1997). Butterfly metapopulations. In I. Hanski, & M. Gilpin (Eds.), *Metapopulation biology* (pp. 359–386). San Diego: Academic Press.
- Tikka, P. S. (1954). Haapametsiköiden rakenteesta ja laadusta. I. Rakenne (Summary: Structure and quality of aspen stands. I. structure). *Communicationes Instituti Forestalis Fenniae*, 44, 1–33.
- Tikka, P. S. (1956). Haapametsiköiden rakenteesta ja laadusta. II. Laatu (Summary: Structure and quality of aspen stands. II. Quality). *Communicationes Instituti Forestalis Fenniae*, 45, 1–54.
- Tilman, D., & Kareiva, P. (Eds.) (1997). *Spatial ecology*. Princeton: Princeton University Press.
- Uotila, A., Kouki, J., Kontkanen, H., & Pulkkinen, P. (2002). Assessing the naturalness of boreal forests in eastern Fennoscandia. *Forest Ecology and Management*, 161, 257–277.
- Uotila, A., Maltamo, M., Uuttera, J., & Isomäki, A. (2001). Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological Bulletins*, 49, 149–158.
- Väisänen, R. A., Järvinen, O., & Rauhala, P. (1986). How are extensive, human-caused habitat alterations expressed on the scale of local populations in boreal forests? *Ornis Scandinavica*, 17, 282–292.