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BIOTA AND PERSISTENCE OF RETENTION TREES IN RELATION TO THE CHARACTERISTICS OF THE TREES AND CUT AREAS

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers, which are referred to by the Roman numerals in the text. The papers are reproduced by kind permission of the publishers.

I   **Rosenvald, R**., Lõhmus, A., 2007. For what, when, and where is green-tree retention better than clearcutting? A review of the biodiversity aspects. Forest Ecology and Management, published online Oct. 15, 2007. DOI: 10.1016/j.foreco.2007.09.016.

II   Lõhmus, P., **Rosenvald, R**., Lõhmus, A., 2006. Effectiveness of solitary retention trees for conserving epiphytes: differential short-term responses of bryophytes and lichens. Canadian Journal of Forest Research 36, 1319–1330.

III   **Rosenvald, R.,** Lõhmus, A., 2007. Breeding birds in hemiboreal clear-cuts: tree-retention effects in relation to site type. Forestry, published online Sept. 13, 2007. DOI: 10.1093/forestry/cpm027.

IV   **Rosenvald, R**., Lõhmus, A., Kiviste, A. Short-term determinants and long-term prospects of retention-tree survival in hemiboreal cut areas. Submitted manuscript.

The contributions of the authors of the papers were as follows:

	I	II	III	IV
Original idea	AL	AL	AL, RR	AL, RR
Study design	AL, RR	AL, PL, RR	AL, RR	AL, RR
Data collection	RR	RR, PL	RR, AL	RR
Data analysis	RR, AL	AL, PL, RR	RR, AL	AK, RR, AL
Manuscript preparation	RR, AL	PL, AL, RR	RR, AL	RR, AL

AK – Andres Kiviste; AL – Asko Lõhmus; PL – Piret Lõhmus; RR – Raul Rosenvald.

ABBREVIATIONS

GTR – green-tree retention cutting
VRC – variable retention cutting
CWD – coarse woody debris
GLM – general liner model
DBH – diameter at breast height

1. INTRODUCTION

In the last decades, forestry has been increasingly focusing on multiple values instead of timber production only. Changes began largely after the United Nations Conference on Environment and Development in Rio, 1992 (Johnson, 1993). The principles presented there recognised the simultaneous roles of forests in economic development, in the preservation of biological diversity, as a carbon reserve retarding the global warming process, for soil and water protection, and as a source of cultural and spiritual values important for the mankind. Of these, "biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems (The Convention on Biological Diversity: Johnson, 1993).

Following the Rio conference, the Pan-European Conferences (Helsinki 1993, Lisbon 1998 and Vienna 2003) have verified and refined the principles for forest management and, gradually, the whole aim of forestry has been transformed – to preserve biodiversity and other forest-related values while retaining economic viability (Franklin et al., 1997; Lindenmayer and Franklin, 2002). A general term for the resulting modifications of conventional silvicultural methods is "sustainable forestry" (see Kimmins, 1995; Larsen, 1995; Kerr, 1999; Anonymous, 2003), sometimes also "the new forestry" (Franklin, 1989). In the current Estonian forest policy, sustainability is one of the two leading principles, defined as the management of forests in a manner and to the extent that maintains their biological diversity, productivity, capacity for regeneration and vitality as well as their potential to fulfil, at present and in the future, ecological, economic and social functions at the local, national and global level without damaging other ecosystems (Anonymous, 2003).

The most widespread approach for reaching sustainable forestry from the aspect of biodiversity has been to use silvicultural techniques that imitate natural disturbances (e.g., Hunter, 1993). The clearest difference between the conventional forest management technique – clear-cutting – and a natural disturbance is that clear-cutting attempts to remove as much wood as possible, while after a fire, windstorm or disease many legacies of the previous forest structure remain at place, and the resulting structural complexity plays an important role in the functioning of

the forest's ecosystem and for biodiversity (Lindenmayer and Franklin, 2002). Thus, the similarity between clear-cutting and natural disturbances could be increased if structural features of old forests, such as live and dead trees of varying sizes, multiple canopy layers, and coarse woody debris, are purposefully retained on cuts (Franklin et al., 1997; Beese et al., 2003). However, corresponding variable retention harvest system is a disturbance in a dynamic forest landscape creating habitats for pioneer species and modifying succession patterns afterwards. Therefore, given that the conditions after stand-replacing disturbances differ from those within forest by definition, comparing VRC cuts with forests (as has often been done) is of secondary importance. Instead, the main question is how forest biota survives in the landscape despite or because of such intensive disturbances. Consequently, the aim of retention trees is sustaining the populations or communities which are lost in the conventional clear-cutting forestry (Lindenmayer and Franklin, 2002). Franklin et al. (1997) list the three main objectives of VRC: (1) 'lifeboating' species and processes over the regeneration phase, (2) enriching re-established forest stands with structural features, and (3) enhancing landscape connectivity. The structural enrichment objective can be further divided into long-term and short-term enrichment according to the results of many studies on the importance of the latter for disturbance-phase species (e.g. Hansen et al., 1995; Kaila et al., 1997; Martikainen, 2001). Thereby, the main attention on live trees (GTR) is due to the dependence of long-term existence of other structures on them as well as the most pronounced conflict with timber production objectives.

Since 1999, the Estonian Forest Act requires the retention of three types of trees in clear-cuts: (1) seed-trees, which will be cut later, (2) live trees having high-quality timber for future cutting (termed *säilikpuu*, i.e. retention tree), (3) live and dead trees „for biodiversity" (at least 5 m^3 per hectare) (Anonymous, 1999, 2007). This restriction of the term "retention tree" for category (2) above differs from the conventional approach adopted elsewhere in the world. Given the international scope, this study defines retention trees as trees for biodiversity which stay in a forest permanently (category 3 above). However, before cutting, also the trees of categories (1) and (2) support wildlife and they can be difficult to distinguish from true retention trees in the field. Therefore, in original studies **II–IV**, all trees standing were considered retention trees for the aims of these studies.

This study stems from the notion that, so far, there has been no overview of the worldwide use of the tree retention, of the studies conducted, and of the effectiveness of retention trees. Here, for the first time, such a review was compiled, problematic gaps of knowledge were distinguished, and some of them were filled with specific case studies.

2. REVIEW OF THE LITERATURE

Literature is thoroughly reviewed in paper **I**; hence, the section below presents only a historic summary about tree retention, the amount of research and research needs.

2.1. History of tree retention and the research efforts

The retention of live trees during cutting has been in use for a very long time, but with aims other than biodiversity – better regeneration of desired tree species in cut areas, valuable timber in the future, aesthetic reasons or protection of forest ground or water bodies (e.g. Brosofske et al., 1997; Hannerz and Hånell, 1997; Jakobsson and Elfving, 2004; Valkonen et al., 2002). However, its value for biodiversity has been extensively recognised only during the last decades (Hansen et al., 1995; Franklin et al., 1997; Vanha-Majamaa and Jalonen, 2001). The retention of standing dead trees for wildlife has somewhat longer history: for example in the USA, it came into practice in the middle of the 1970s, and became widespread in the beginning of the 1980s (Davis et al., 1983).

Leaving both live and standing dead trees for biodiversity on the cut, as an attempt to mimic and restore natural disturbance, began mostly in 1980s (Franklin, 1989; Franklin et al., 1997). Today, it is widely used all over the world. Those trees can be called retention trees, residual trees or wildlife trees. The corresponding silvicultural systems are mostly known as variable retention cutting (VRC) (Franklin et al., 1997), including green-tree retention (GTR) – the retention of live trees (e.g. Beese and Bryant, 1999; Vanha-Majamaa and Jalonen, 2001) – and various names for particular techniques. Often the trees are retained in groups, which reduces harvest costs and windthrow hazard, and may further benefit biodiversity (Franklin et al., 1997).

Research on GTR became systematic in the late 1980s (Figure 1 in **I**) and has reached a phase of integration now. For example, several large-scale field studies have been initiated in North America (Monserud, 2002) and the Fennoscandian experience has been summarized (Vanha-Majamaa and Jalonen, 2001). A summary of the study issues and objects related to biodiversity is given in Table 1.

Table 1. Numbers of green-tree retention studies according to main issues, objects and geographical region (A – North America, E – Europe). Brackets indicate long-term studies (at least 20 years post-cut) (**I**)

Study issues and objects	Region					Total
	Boreal		Temperate		Sub-tropical	
	A	E	A	E	A	
Biodiversity effects [1]	49	22	60	3	10	144 (28)
Epiphytes	1	4	4	1		10 (3)
Ground vegetation	7	6	12			25 (5)
Ectomycorrhizal fungi	5	1	5			11 (2)
Arthropods	5	11	3		1	20 (2)
Amphibians and reptiles			6		1	7
Birds	22		19	2	5	48 (10)
Mammals	9		11		3	23 (6)
Effects on retention trees and regeneration	38	16	45	2	8	109 (28)
Stand regeneration	13	6	18	2	5	44 (13)
Growth of retention trees	3	2	12		2	19 (10)
Stand structure [2]	4	5	5			14 (5)
Wind-resistance	15	2	3			20
Logging damage on trees and soil	3	1	7		1	12
Other ecological and biological effects [3]	10	4	5		1	20
Total	97	42	110	5	19	273 (56)

[1] incl. 5 studies on bird nest predation, 2 on mammal diets (all in North America)

[2] incl. 3 studies on GTR as a source of coarse woody debris (all in boreal Europe)

[3] incl. 6 studies on the production, germination, dispersal or predation of tree seeds; 4 studies on GTR effects on genetic structure of regeneration; 5 studies on the changes in microclimate and 5 studies on the changes in soils

2.2. Research needs

Despite the extensive research already done (Table 1), the purposes and objects of the GTR studies have been often disputable. We defined (**I**) three main gaps of research, some of which the case studies (**II–IV**) tried to fill.

1. The studies should be objective-oriented and, consequently, have a clear ecological reasoning for the selection of study taxa. In particular, it is unknown to which extent live retention trees improve the landscape connectivity (i.e. dispersal) for relevant species groups (e.g. mobile animals with large home-ranges or the species with pronounced extinction-immigration dynamics). Also, there is a shortage of short-term (lifeboating) studies on poor dispersers and disturbance-phase species (e.g. Peck and McCune, 1997).

2. Spatially explicit landscape perspectives on GTR as a biodiversity protection tool are urgently needed, particularly with regard to (1) the viability of threatened species, which at the scale of individual cuts are so rare that statistical power to detect any effects has been extremely low (Angelstam et al., 2004a); (2) applying varying retention levels according to presumable disturbance regimes in different site types to find adaptations according to the regimes (Schmiegelow et al., 1997; Lõhmus et al., 2004), and comparing the biodiversity effects with fixed-level retention (Franklin et al., 1997). Additionally, the effects of GTR should be compared in forest landscapes with different histories (see Robinson and Robinson, 1999).

3. There is a need to expand the time-scale of studies (e.g. Franklin et al., 1997; Hazell and Gustafsson, 1999), particularly to assess the objective of long-term structural enrichment, which may be more crucial than temporary lifeboating for forest biota in dynamic landscapes (Lõhmus and Lõhmus, 2007). In addition to the few pioneering projects in the western United States and Canada (Monserud, 2002), long-term studies are needed in other forest regions and continents, including retrospective research in areas where ancient trees, comparable to the present-day retention trees, have been traditionally protected in managed forests. In addition to the biota, it is necessary to explore the persistence of live retention trees themselves, which is the precondition for their effectiveness in structural enrichment of the re-established forest stands. The only prediction published so far (Busby et al., 2006) is based only on the estimates from two years and neither better survival prospects in forests nor cuttings were taken into account.

3. AIMS OF THE STUDY

In the last decades, in many places over the world, including Estonia, trees have been retained during cutting. The aim of such trees is to enhance biodiversity by mimicking natural disturbance, where almost always the structural elements remain in place. The actual benefit of retention trees, as previously discussed, is not clear. The aims of this study were:

1. To review live-tree retention according to the results of previous studies in order to study the efficacy of its different objectives for biodiversity conservation (**I**);
2. To test short-term benefits of tree retention for different species groups and species, the persistence of retention trees, and to find additional factors affecting them (**II–IV**);
3. To predict whether and to which extent the live retention trees are likely to fill their aims in the future (**I, IV**).

4. MATERIAL AND METHODS

4.1. Material and areas

Paper **I**, based on 214 North American and European studies, explores whether, and under which circumstances, VRC meets its objectives (sensu Franklin et al., 1997). The publication list was compiled mostly by searching electronic databases and reference lists for reports and reviews, which had been published from the beginning of 1981 to August 2006. The studies described situations where (1) trees had been harvested for timber production from at least 1 ha of mature forest, (2) at least four trees ha^{-1}, but no more than 50% of pre-harvest numbers, had been retained solitarily or in up to 1-ha patches for any purpose, and (3) effects of retained trees on biodiversity or the structure of the stand had been measured.

The original studies (**II–IV**) were carried out in Estonia, Northern Europe. Persistence of retention trees (**IV**) was studied in 102 VRC areas, lifeboating of epiphytes (**II**) – in 85 VRC areas and in adjacent forest, and birds (**III**) – in 77 VRC or clear-cuts.

All original studies included, partly or in full, the set of 102 stands that had been harvested during 2001–2002 in four randomly selected state forest districts in Central (Kõpu and Kabala districts) and Southern (Laeva and Alatskivi districts) Estonia (between 58–59°N and 25–27°E; altitude below 75 m a.s.l.; Figure 1). All studied districts comprised large extensively managed forest areas. According to the pre-cut stand, the cuts were classified (according to Lõhmus 1984) into four main types: (1) oligotrophic – nutrient-poor dry *Pinus*-dominated forests (*Vaccinium vitis-idaea* and *Vaccinium myrtillus*-type) (n = 7); (2) mesotrophic – mixed forests of *Oxalis*, *Oxalis-Vaccinium myrtillus* and *Hepatica*-types (n = 25); (3) eutrophic – mostly deciduous forests mixed with *Picea*, belonging to *Aegopodium*- and *Filipendula*-types (n = 58); (4) swamp – both mobile- and stagnant-water stands, but all drained to some extent (n = 12). The age range of the pre-cut stands had been mostly between 50 and 80 (maximum 110) years for deciduous stands and between 90 and 110 (maximum 180) years for conifer stands. The mean area of the cuts was 2.3 ha (range 0.3–6.9 ha); the post-harvest live tree density was 15.9 trees ha^{-1} (range 2.3–47.5 trees ha) and the density of dead trees and snags was 3.8 trees ha^{-1} (range 0–18.9 trees ha). Most retained trees were solitary. In the four districts, 33% of the live trees on VRC cuts were birches (*Betula*

spp.), 20% were Scots pine (*Pinus sylvestris* L.), 18% were European ash (*Fraxinus excelsior* L.), 15% were European aspen (*Populus tremula L.*), 7% were littleleaf linden (*Tilia cordata* P. Mill.), and 7% were other species. Of the dead trees, 44% were birches, 17% Norway spruce (*Picea abies* L. Karst.), 14% aspen, 10% grey alder (*Alnus incana* L. Moench), 9% Scots pine, and 6% were other species. The average post-harvest diameter was 30.2 cm (range 14–100 cm) for live trees and 25.0 cm (range 14–75 cm) for dead trees; their volumes per hectare being 15.7 m^3 (range 1.5–60.2 m^3) and 1.3 m^3 (range 0–12.3 m^3), respectively.

For studying the avifauna of the cuts (**III**), 28 cuts were selected from among the 102 previously mentioned cuts, while 49 cuts were studied in the frame of another research program (Figure 1). The average area of the cuts in this study was 3 ha (range 0.4–8 ha); they had been harvested on the average 4.9 years (range 2–12 years) prior to the study. During the fieldwork there were on the average 11.7 (range 0–100) live trees and 3.1 (range 0–24) dead trees ha^{-1}. Of the live trees, 42% were Scots pine, 18% birches, 11% European aspen and 13% rare hardwoods (European ash; *Ulmus glabra* Huds.; *Quercus robur* L.; *Acer platanoides* L.). Of the dead trees, 37% were birches, 22% European aspen, 17% Scots pine, 13% Norway spruce and 8% grey alder. The average diameter was 28.8 cm (range 14–84 cm) for live trees and 27.7 cm (range 14–84 cm) for dead trees; their volumes per hectare were 10.1 m^3 (range 0–74 m^3) and 1.2 m^3 (range 0–8.6 m^3), respectively.

Figure 1. Location of the study areas: the four forest districts with the experimental areas of papers **II-IV** (ovals) and the additional regions where only birds (**III**) were studied (squares).

4.2. Field data

Field data were collected between 2002–2007. In spring 2002, all live and standing dead trees (incl. broken-top snags ≥2 m tall) with ≥14-cm diameter were mapped in field; their species, DBH (also height for snags) and condition were recorded, and the site type and size of the cuts were determined. Every next year until 2007, the cuts were examined in summer to record the survival of each tree, the type of damage if present, and (in case of snags) also any changes in their height (**IV**).

In 2003 and 2004, epiphytic lichens and bryophytes were investigated on Scots pine, birch, European aspen and ash; additionally, three locations on the landscape (the centre and the edge of the clear-cut) and the adjacent forest were distinguished (**II**). Species composition, abundance and species-specific vitality were visually assessed for whole trunks between heights of 0.2–2 m. Species-specific vitalities were coded according to Hedenås and Ericson (2003; slightly modified): 0, no change in colour and thus no desiccation damage; 1, few visible colour changes; 2, large patches with colour changes; 3, severe bleaching or thalli/stems either dead or lost. More accurate numerical estimates (incl. total coverage and vitality estimates) were obtained from 20×20 cm plots, which were placed at heights of 1.3 and 0.2 m on the northern and southern sides of the trunks. The general vitality estimates were based upon clearly visible changes in the colour and structure of thalli or stems and were quantified as the share of the desiccated part of the total cover.

Birds were censused in 2004, 2005 or 2006 using standard two-visit surveys (**III**). We additionally visited more than half of the cuts, representing all site types and retention levels, in the evening of the same or preceding day to find previously undetected pairs and nests. The position of singing males, nests or (in the absence of these) any other observations referring to nesting were recorded on a topographic map (scale 1:2000–1:3000). The abundance of each species in each site was determined as the maximum count plus probable or confirmed nestings in clearly different locations during the other visit. Territorial birds moving across site borders as well as adult individuals of species with large home range or unstable pairs were counted as 0.5 pairs (Lõhmus and Rosenvald, 2005). Trunk volumes of the trees, logs and snags were estimated (**III–IV**) according to species-specific diameter-functions (Padari, 2004).

4.3. Data processing and statistics

Conventional parametric statistics (t-test, ANOVA, GLM**) (I–III**), or – if the assumptions of parametric tests were not met – non-parametric statistics (Wilcoxon's test, Kruskal-Wallis ANOVA, χ^2-test, Spearman correlation) (**II–IV**) were used for hypothesis-testing. For parametric tests, the relevant variables were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test), and transformed where appropriate: arcsine-square-root transformation was used for proportions (**II**), and square-root or logarithmic transformation for other variables (**I–III**). Logistic regression was used for building multivariate explanatory models (**III–IV**). The strategy of logistic regression modelling followed Hosmer and Lemeshow (1989, **III**) or Littell et al. (2002, **IV**).

In two papers, the key variables were ratios. (1) To evaluate the differences in biodiversity condition in clear-cuts and GTR cuts in the meta-analysis (**I**), the differences were presented as logarithmed ratios $R = \ln (g/c)$, where g is the average value in GTR cut and c is the value in clear-cut. (2) To evaluate the impact of VRC on epiphytes (**II**), exponential rate of vitality change of thalli (v) within two years on each tree was calculated as $v = \ln (A_2(1-p_d)/A_1)$, where A_1 and A_2 are total coverages of lichens or bryophytes one and two years after the harvesting, respectively, and p_d is the damaged proportion of the total cover in the second year.

For rough projection of the retention-tree population (**IV**), the annual post-cut mortality was modelled as decreasing linearly from estimates of the 1st post-cut year mortality (**IV**) to the mortality rates of large (DBH >20 cm) forest trees in two permanent plots in Estonia (see Kiviste et al., 2005), and stabilizing at that level. The latter datasets distinguished natural deaths and cutting (thinning). Four scenarios were calculated: (1) maximum survival with natural mortality only – the better survival estimates for both retention trees and forest trees, assuming that that the stable survival typical to forests will be reached in 30 years; (2) minimum survival with natural mortality only – the worse survival estimates and a duration of 40 years to reach stable survival; (3) maximum and (4) minimum survival with thinnings – similar to scenarios (1) and (2), respectively, except that the survival of forest trees included the cuttings.

Most analyses were performed with the Statistica 6.0 software (StatSoft Inc., 2001); for multilevel logistic regression (**IV**), the data were analysed by fitting mixed generalized linear models (SAS PROC GLIMMIX; Littell et al. 2002).

5. RESULTS

5.1. Meta-analysis and review of previous studies on GTR (I)

Altogether, 214 studies on biodiversity or other ecological effects of GTR were found (**I**). Distribution of the studies in time- and space-scale was unbalanced: 81% of them had been carried out in North America and 82% had been short term.

5.1.1. General effects of GTR

Published GTR effects (compared with clear-cutting) on species richness and abundance of different taxa indicated no negative responses, but birds and ectomycorrhizal fungi benefited most (Figure 2). No retention level was worse than clear-cutting, and significant positive effects of GTR appeared for the highest levels, i.e. retaining of more than 15% of the growing stock (Figure 3 in **I**).
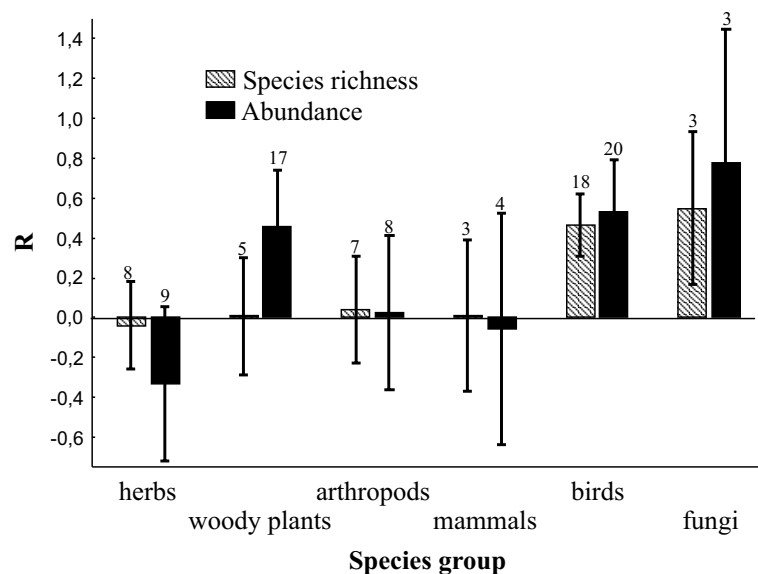

Figure 2. Mean differences between GTR-cuts and clear-cuts in the species richness and abundance of different species groups. R – natural logarithm of ratio of the values in GTR-cuts vs. clear-cuts (positive values indicate higher values in GTR cuts); labels indicate the number of studies; lines are 95% confidence intervals for the mean (**I**).

5.1.2. GTR objectives, research and effectiveness

As compared to clear-cutting, statistically significant improvements in the post-cut survival of populations or individuals on GTR sites (lifeboating) were reported in 72% of the 57 studies (Table 2 in **I**). The effectiveness depended on taxon (see also Maguire et al., 2005; **II**): it was best for ectomycorrhizal fungi, epiphytic lichens and small ground-dwelling animals such as carabid beetles, salamanders, and the vole *Clethrionomys gapperi*. In contrast, GTR was usually insufficient to preserve forest bryophytes (both epiphytic and epigeic species) and vascular plants (Table 2 in **I**) in the post-cut site. For disturbance-phase species (short-term structural enrichment), retention trees improved the cut areas in 76% of the 37 case studies: seldom for mammals, but always for insects and usually for birds (Table 2 in **I**). Long-term or retrospective records, which linked the stand structure to the biodiversity response (long-term structural enrichment), detected significant benefit from GTR in 13 out of 14 results (93%) on relevant taxa (Table 2 in **I**). Improving landscape connectivity appeared to be not studied.

5.1.3. Technical considerations for successful GTR

For disturbance-phase species, even smaller-scale requirements of GTR remain unclear because silvicultural studies have not distinguished these taxa. For forest species, four technical aspects could be summarized – tree density, grouping, species and site type (Table 2 in **I**). Among these, retention-tree species was always a significant factor and thus should be of primary concern, followed by tree density (statistically significant in 65% of cases). The spatial arrangement of the trees had less importance (50%) on forest biodiversity, and the influence of forest type – although central for the disturbance-mimicking paradigm (Fries et al., 1997) – has remained nearly unexplored according to our review.

5.2. Original studies: filling the gaps
5.2.1. Lifeboating lichens and bryophytes (II)

The damages on retention trees were severe and independent of tree species for bryophytes throughout clear-cuts (Figure 3 in **II**), but weak for lichens, particularly at the cut edge, and on aspen and ash (Figure 2 in **II**).

On average, 2% of lichen thalli, but 60% of bryophyte stems became damaged in two years. Similarly, while retention trees and forest trees hosted similar total numbers of cryptogam species and mean numbers of lichen species per trunk, on average 1.1 bryophyte species per trunk were lost on retention trees (paired t-test: $P < 0.001$).

Also the relationships between the average damage scores of the same species on retention trees and forests trees were different for lichens and bryophytes (Figure 3). For lichens, the damages were mostly explained by the general sensitivity of certain species. Crustose lichens and some macrolichens with small foliose or podetial thalli (e.g. *Cladonia coniocraea*, *Vulpicida pinastri*) were in remarkably good condition. For bryophytes, the damages in clear-cuts greatly exceeded those in forests, particularly for the species that were relatively vital in forests (e.g. *Homalia trichomanoides*).
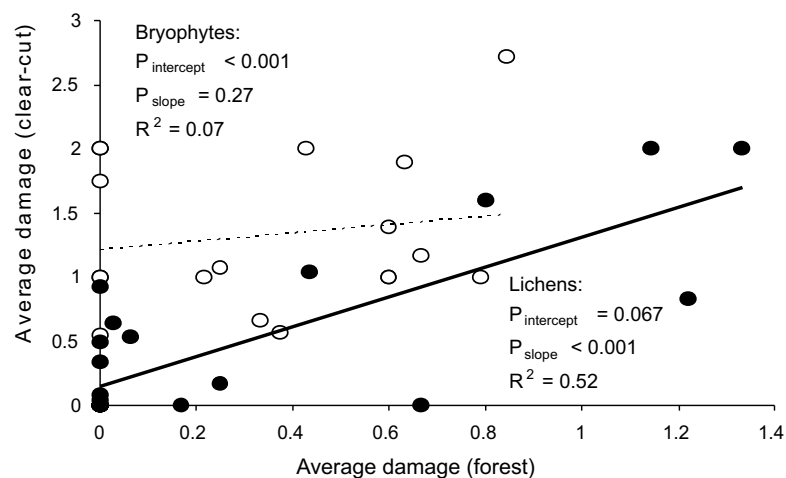

Figure 3. Linear regressions between the average damages on forest and retention trees for 19 bryophyte (circles) and 24 lichen species (filled dots) (**II**).

5.2.2. Short-term structural enrichment for birds in relation to site type (III)

In cut areas, the total breeding bird densities were explained with two alternative models (Table 2), both of which included site type (highest densities in swamp sites, lowest in oligotrophic sites; Figure 1A in **III**). The first model revealed the bird density increase along with dead-tree volume (Figure 2A in **III**). Alternatively, model II showed that smaller

cuts had higher bird densities (Table 2). The relative avian species richness (adjusted to area) was a function of site type (Figure 1B in **III**), dead tree volume (Figure 2B in **III**), and more tree species on the cuts (Table 2).

Table 2. General linear models explaining the density of all breeding birds and their relative species richness (adjusted to area) in 77 cuts, and the density of hole-nesters in 53 retention cuts (**III**).

Model and variable	Coefficient (mean ± SE)	F	P
Density, no. of pairs ha^{-1}			
I. ($R^2 = 0.25$, $F = 6.0$, $P < 0.001$)			
Site type		6.47	<0.001
Volume of dead trees ha^{-1}	0.61 ± 0.27	5.29	0.024
II. ($R^2 = 0.25$, $F = 6.0$, $P < 0.001$)			
Site type		5.21	0.003
Area	-0.23 ± 0.1	5.10	0.027
Relative species richness ($R^2 = 0.35$, $F = 7.6$, $P < 0.001$)			
Site type		5.38	0.002
No. of tree species	0.31 ± 0.13	6.16	0.015
Volume of dead trees ha^{-1}	1.31 ± 0.54	5.89	0.018
Density of hole-nesters, no. of pairs ha^{-1}			
I. Site type ($R^2 = 0.16$, $F = 3.1$, $P = 0.037$)		3.05	0.037
II. No. of tree species ($R^2 = 0.11$, $F = 6.1$, $P = 0.017$)	0.24 ± 0.1	6.11	0.017

Note that there are two alternative models (referred to by Roman numerals) for the density of all birds and the density of hole-nesters.

Among the species groups of particular concern, the density of hole-nesters in the 53 retention cuts was explained by two alternative univariate relationships with variables dependent on each other (Table 2; Appendix A in **III**). The influence of site type contained a significant contrast between mesotrophic and oligotrophic sites (Figure 1C in **III**). The positive effect of tree-species richness disappeared when site type was taken into account.

The species of national conservation concern (according to Eesti Ornitoloogiaühing, 2001) nested in 25 cuts of the 77 (32%); preferably in larger cuts with higher densities of live trees (Figure 4). The species of conservation concern and hole-nesters preferred the cuts having the most species-rich avian communities, hole-nesters prefering also the cuts with densest avian communities.
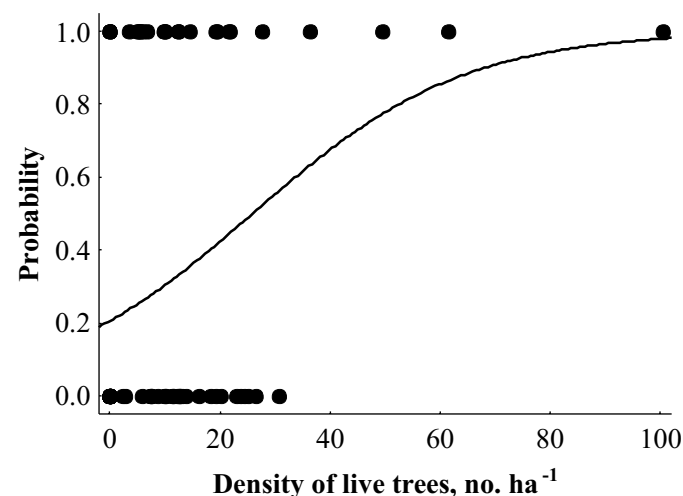

Figure 4. Incidence of the bird species of conservation concern in relation to live-tree densities on the cuts. The presence-absence data are linked with logistic function; the mean area of the cuts was 3 ha (**III**).

5.2.3. Short-term survival of live retention trees: dynamics and determinants (IV)

The total number of live retention trees decreased 35% in six years in the cut areas of 2001, and 36% in five years in the cut areas of 2002. Wind damage comprised 89.6% of tree deaths. The annual mortality rates were,

on average, 6.8 ± 4.6% and 8.2 ± 6.2 %, respectively, and these rates declined in time (Figure 3 in **IV**). The total live-tree volume (m^3 ha^{-1}) was reduced from 13.1 to 7.6 for the 2001 cut areas and from 14.1 to 8.8 for the 2002 cut areas during the study, adding 4.5 m^3 and 4.3 m^3 of downed dead trunks per ha, respectively, and 1 m^3 of standing dead trees per ha in both samples (Figure 4 in **IV**). According to multilevel logistic regression, the main determinants of tree survival were tree species (the best survivors being hard deciduous trees – *Fraxinus, Ulmus, Quercus, Acer, Prunus* and *Sorbus* – and followed by soft deciduous trees – *Alnus, Tilia* and *Salix*), tree position relative to forest edge (best survival near current or former forest edge; Figure 6B in **IV**), post-harvest density of retention trees (positive; Figure 2 in **IV**), and exposure (negative; Table 3; Figure 6A in **IV**). Diameter affected survival (Table 3) depending on tree species: positively in aspen and in soft deciduous trees, and negatively in birch. Without the nesting approach, diameter seemed to have no effect ($F_{1, 3242} = 2.0$; $P = 0.16$).

Table 3. Fixed effects of the multivariate model for the 5–6-year survival of individual live retention trees (**IV**).

Variable	DF	*F*	*P*
Species	5; 3237	6.56	<0.0001
Diameter[a]	6; 3237	4.44	0.0002
Post-harvest density	1; 84.2	7.52	0.0074
Tree position	4; 3237	17.49	<0.0001
FETCH	1; 759.5	11.49	0.0007

[a]nested in species

5.3. Predicted long-term effectiveness of retention trees

The majority of long-term or retrospective records, which linked the stand structure to the biodiversity response on relevant taxa detected significant benefit from retention trees (Table 2 in **I**). Although few studies on the density of retention trees have been conducted, these confirm that a greater number of trees enhance the positive effect on wildlife (**I**). The future tree densities result from retention densities and tree survival, and paper **IV** predicted the latter for Estonian conditions as follows. When we took into account (only) natural mortality in closed middle-aged stands after 30 or 40 years (which we considered the time-line for stable survival typical to

forests), 29–38% of retained live trees were likely to be present after 40 years and 22–29% in 100-year-old stands. When commercial thinning was taken into account in addition to natural mortality in closed stands after 30 or 40 years, these proportions became 18–28% and 9–15%, respectively (Figure 5).
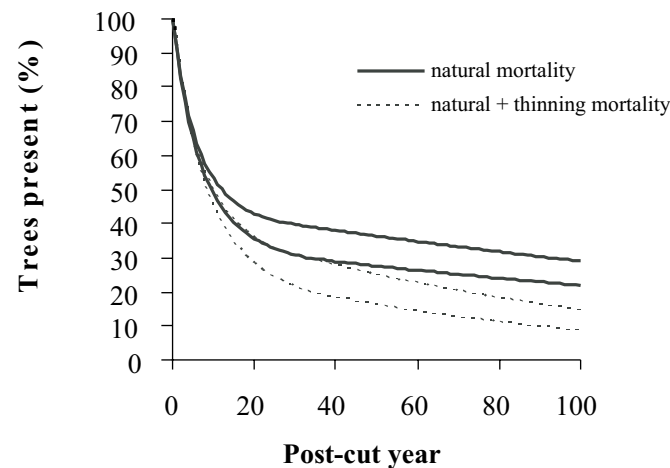

Figure 5. Projected future populations of live trees retained at harvest (minimum and maximum scenarios for each mortality regime) (**IV**).

6. DISCUSSION

6.1. Taxon-specific responses to GTR and the target taxa

We found that tree retention effectiveness depends greatly both on species group and species (**I–III**), e.g. the negative impacts of cutting were severe for bryophytes, but less for lichens (**II**). Other studies have come to basically similar conclusions, but the extent of the impact depends greatly on the species of cryptogam and the density of retention trees (e.g. Beese and Bryant, 1999; Hazell and Gustafsson, 1999; Hedenås and Ericson, 2003). Paper **III** demonstrated that the bird species of national conservation concern clearly depended on live-tree retention (see also Conner et al., 1991; Niemi and Hanowski, 1997) while such a relationship between the density and species richness of all species, and the abundance of hole-nesters was not detected. The latter is particularly noteworthy, because resident hole-nesters have been considered suitable indicators of sustainable forestry in boreal regions: they suffer seriously from modern timber-extraction (Schmiegelow et al., 1997; Imbeau et al., 2001).

The taxon-specificity of GTR effects has important implications for research and practical forest management. So far, the selection of study taxon has been rather random and, considering the objectives of GTR, often not indicative or even relevant (**I**). For example, birds have often been used to detect the effectiveness of short-term lifeboating in a small area, but landscape-scale changes as well as the presence old-growth structural elements in young forests are obviously much more relevant for them. We suggested that the taxa that respond most clearly are suitable for monitoring forest management, i.e. comparing different GTR techniques and assessing the general use of GTR in silviculture. In general, we concluded that ectomycorrhizal fungi and epiphytes depend strongly on lifeboating, and wood-depending insects and disturbance-phase or forest birds probably benefit most due to the structural enrichment (**I**). In contrast, the management-sensitive taxa, whose performance has not been improved with GTR, are the clearest research priorities regarding their viability and further modifications of management techniques to improve it (**I**).

6.2. Retention trees in the context of natural disturbances

To create post-cut habitats that are more suitable for forest biodiversity, cuttings should resemble natural disturbance regimes, such as fire (Hunter, 1993; Steventon et al., 1998). Within the framework of objectives for VRC, we suggested that: (i) it is likely to retain forest species better than fire at the stand scale; (ii) live retention trees alone cannot provide all the fire-created structures for disturbance-phase species (Dahlberg et al., 2001; Hyvärinen et al., 2005; Bradbury, 2006), though they may create woody substrata for thermophilous species (Martikainen, 2001; see also **IV**); (iii) the retention trees may be equal to fire legacy regarding long-term structural enrichment, at least the provision of old live trees (**I**). However, dead-tree retention – a characteristic element of naturally burnt areas (e.g. Schieck and Song, 2006) – is perhaps as important as the retention of live trees or even more important, at least in the short-term perspective. Supporting this, paper **III** found that bird density increased along with dead-tree volume. Yet, it is unlikely that the observed benefits of standing dead trees for birds could result from adaptations to such structural elements and natural disturbances (e.g. Shieck and Song, 2006), since the volumes of retained dead trees in our study were less than 1% of those reported after natural burns (Siitonen, 2001).

At the landscape scale, topography and water regime have created a mosaic of patches with different natural disturbance regimes. Therefore, spatially explicit planning of cutting methods and GTR levels would be required (McRae et al., 2001; Keeton and Franklin, 2004). In Sweden, Fries et al. (1997) suggest a gradient of 5–20 pines ha^{-1} in dry pine sites, variable patterns of dispersed and patchy retention in mesic successional forests, and selection systems or shelterwood retaining one-third of the trees in moist spruce stands.

In testing this hypothesis in paper **IV**, however, we did not find site-type specific survival of live retention trees. This contradicts the common understanding that the trees on wet or fertile soils are relatively wind-prone (Dunham and Cameron, 2000; Ruel, 2000; Mitchell et al., 2001; Vanha-Majamaa and Jalonen, 2001). Similarly, we did not find any interactions between site type and the variables of tree retention relevant to bird community characterictics, though we warn about drawing far-reaching conclusions from this: (1) birds in general may tolerate forestry operations better than many other taxa (Imbeau et al., 2001), particularly

at small scales (Similä et al., 2006); (2) even though birds could guide disturbance-based management at the landscape scale (Angelstam et al., 2004b), they may be less informative in heterogeneous landscapes like Estonia; (3) the low retention levels of the study (mostly up to 5% of growing stock) may not mimic natural disturbances sufficiently well – an explanation provided by Virkkala (2004) for the lack of tree-retention effects on Finnish birds. Also, there can be some confounding factors, such as drainage, in our studies (**IV**).

6.3. Stand-scale management

Among the reviewed studies, tree species appeared to be the most influential technical consideration for biodiversity (**I**). Theoretically, as different tree species host different biotic communities, there can be no universal prioritization for retention (all native tree species should be represented at the landscape scale). However, two complementary preferences for practical use emerged (e.g. **II**): (1) rare tree species hosting threatened biotic communities or those with particular qualities not found in the other tree species in that landscape; (2) tree species with high future value for biodiversity, resulting from low mortality and quick development of important features on GTR-cuts (**IV**). For example, large aspens (*Populus* spp.) or hardwoods with coarse bark are priority trees for conserving epiphytic lichens (Hazell et al., 1998; McGee and Kimmerer, 2002; **II**). Importantly, despite their significant effects for biodiversity and tree survival acknowledged in many studies (referred to in **I, II**, **IV**), tree-scale characteristics other than species (such as age, size or shape of the crown) have received almost no attention (**I**).

The optimum density and spatial configuration of retention trees have been listed among the most important questions for VRC research (Franklin et al., 1997). No general answer has been provided so far, and our meta-analysis confirmed the lack of such research (**I**). However, it seems that group retention is generally better for biodiversity (**I**) and, at higher levels of retention, additional positive effects appear both for biota (**III**; Figure 3 in **I**) and the survival of retention trees (e.g. Beese 2001; Walter and Maquire, 2004; Scott and Mitchell 2005; **IV**).

The decline of tree survival from the oldest (field) to medium-aged (road) and young pre-cut edges (previously cut area) as well as cut interior

indicated time-limited adaptation of trees with wind. Hence, although no other previous works have pointed out tree location relative to pre-cut edge, our study shows that this is the key variable to be considered at the stand-scale to enhance wind-resistance (**IV**).

6.4. Predicted effectiveness of retention trees in the future

Specific parts of forest wildlife appear to have adapted with very old trees in forests (**I**). For such species – even if they could not be continuously maintained – tree retention increases occupancy time in regenerating stands, which is particularly important in short-rotation forestry (e.g. Mazurek and Zielinsky, 2004). For example bryophytes – poorly surviving on the cuts in the short term – are obviously able to re-occupy young stands in the presence of substrata and source populations nearby (Lõhmus and Lõhmus, 2007). Also, the abundance of late-seral birds in GTR stands is likely to exceed that in clear-cut stands during the period between canopy closing and about 100 post-cut years (Hansen et al., 1995). In timber-harvesting areas, some threatened bird species, such as the Spotted Owl (*Strix occidentalis*) or the Red-cockaded Woodpecker (*Picoides borealis*) in North America, may be viable only if residual trees are available for their nesting or foraging (e.g. Franklin et al., 1997; Phillips and Hall, 2000). Also, the endangered Black Stork (*Ciconia nigra*) in Estonia nests on very old trees for nesting, the scarcity of which can be decreased with tree retention (Lõhmus et al., 2005).

Thus, the presence of retention trees in the forest landscape can have a positive effect on biodiversity in the very long-term. Apparently, the low survival of retention trees can decrease their effectiveness for biodiversity, especially if their initial number is small like in Estonia (IV). Hemiboreal old-growth forests normally contain 10–20 large (DBH>70) live trees per hectare (and many more have DBH >50 cm; Nilsson et al. 2002). Retention trees can grow into such large trees, but in order to achieve the desired number of such retention trees that survive in old forest long-term, their initial number per hectare should be increased, taking into account their mortality rate in the meantime. However, very little is known about the long-term survival of retention trees (Busby et al. 2006, **IV**). In paper **IV** we tried to predict the long-term survival of retention trees and assumed that a stable survival typical to forests will be reached in 30 or 40 years (see Lõhmus et al. 2004 for a similar assumption). However, we do not actually know the accurate time line, and probably survival rate stabilises gradually within a longer time frame, not suddenly (see Figure 5). Moreover, survival can be influenced by many additional, unpredictable factors, e.g. occurance of big storms (Beese 2001; Busby et al. 2006). Therefore, our prediction may not be very precise. On the other hand, it is based on more factors than the only other previously published prediction (Busby et al. 2006). The accuracy of our prediction should be tested in field studies in the future. To enhance the prospects of the retention trees of reaching the next forest generation, the most wind-resistant trees should be chosen for retention trees (**II**), and the initial amount of retention trees should be increased (**IV**). The latter is necessary also for the purpose of providing sufficient amount of dead trees. In the hemiboreal old-growth forests the average volumes of CWD are around 100 m³/ha (Siitonen, 2001), while the minima for threatened polypore fungi are 20 m³/ha (Penttilä et al., 2004). Currently, the volume of CWD from retention trees remains considerably below these numbers (**IV**).

6.5. Practical implications

The main aspects to be considered in GTR, and monitored with biological indicators, are the species and size composition of retention trees, retention density, and the position of GTR stands on the landscape. Considering the taxon-specificity of effects, we suggested that ectomycorrhizal fungi, epiphytes, birds, and wood-dependent beetles may be suitable indicator taxa for measuring the success of GTR (**I**). For that purpose it is necessary to study both composition of all species and cut-sensitive species survival in GTR cuts.

The greater diameter of retention trees often enhances their value for biodiversity (**I–II**), while the best survivors among retention trees in Estonia are hard deciduous trees (mostly *Fraxinus, Quercus, Ulmus* and *Acer)* and soft deciduous trees (mostly *Alnus* spp.) (**IV**). Especially, European ash had a relatively high cover of cryptogams, and lichens certainly survived best there (**II**). However, European aspen is also valuable because of its unique and rare species composition (**II**) and a greater diameter than that of other trees (**IV**).

The majority of studies have found that the effectiveness of retention trees for conserving and enhancing biodiversity and tree survival are

enhanced with their density (**I**, **III**, **IV**), and the typical amount retained today in Estonia and Scandinavia (Vanha-Majamaa and Jalonen, 2001) is insufficient both in the short and long term (**I, III, IV**). Notably, the bird species of national conservation concern preferred to nest in cuts with higher density of live trees (**III**). The meta-analysis of GTR also demonstrated that retention levels exceeding 15% of the growing stock (Figure 3 in **I**) had significant positive effects (**I**). We recommend that the density of retention trees should generally exceed this level.

To retain as many trees as possible for the next forest generation, we also recommend to select retention trees which have previously adapted to winds (trees on the edge of fields, roads or earlier cuts) in open sites, and – for preserving forest-interior species – the better-shaded trees near existing forest edge (**IV**). Furthermore, it is recommended to retain trees in groups whereby their value for biodiversity is increased (**I**), and to increase their wind-resistance (**IV**). For all this, as well as for diminishing negative effects of cuttings for sensitive species groups (**I**), landscape-scale silvicultural planning is advisable. On the other hand, since we did not find that the survival or biota of the retention trees in VRC were differently affected in site types with different disturbance regimes (**III-IV**), there is no reason to state that GTR in wet site types is inefficient. More generally, we found no confirmation to the hypothesis that biota in different site types have adapted differently at the scales or extents of our GTR-studies.

7. CONCLUSION

1. The review of 214 North American and European publications about live-tree retention (GTR) (**I**) confirmed that geographic areas, temporal ranges and objectives have been very unevenly covered: 81% of the studies have been carried out in North America, 82% have been short term, and – in contrast to the lifeboating and structural enrichment objectives – the objective of improving landscape connectivity has not been studied.

2. The meta-analysis about the impacts of retention trees to biodiversity (**I**) revealed no negative effects on the species' richness and abundance, but birds and ectomycorrhizal fungi benefited most.

3. Seventy-two percent of the previous studies indicated that, compared with clear-cutting, GTR lowered the harvest-related loss of populations or individuals, and it nearly always improved the habitat for disturbance-phase insects and birds on the cuts and for forest species in the regenerated stand. Lifeboating was most successful for ectomycorrhizal fungi, epiphytic lichens and small ground-dwelling animals, and least successful for bryophytes and vascular plants. The findings were verified in a case study **II** where the damage on epiphytic lichens on clear-cuts was 30 times less than on bryophytes.

4. The success of GTR appeared to be always related to the retained tree species. A case study **II** showed that aspens (*Populus tremula* L.) and ashes (*Fraxinus excelsior* L.) preserve lichens better than other trees. Tree density affected the benefits for biodiversity in 65% of the previous studies; here, in a case study on birds, that was true for species of national conservation concern, but not for total abundance and species richness. The impact of the spatial arrangement of the trees is not clear, but 50% of the previous studies have found it important for the biodiversity. Among insufficiently studied aspects, the variability of natural disturbance regimes implies that retention cutting, aimed at emulating natural disturbances to support biodiversity, should be forest-type specific. In contrast to that expectation, tree retention influenced birds independently of forest type in study **III**, and we also failed to find

better survival of retention trees (**IV**) in site types with frequent natural disturbances.

5. The main determinants of survival (**IV**) were tree species (best in hard deciduous trees – *Fraxinus, Ulmus, Quercus, Acer, Prunus* and *Sorbus*) and diameter (species-dependent effects), tree position relative to forest edge (best near current or former forest edge), post-harvest density of trees (positive), and exposure (negative). The total number of live retention trees decreased 35% in six years in the cut areas, but the mortality rates decreased in time. According to the predictions for different scenarios, 9–29% of retention trees might survive in 100 years.

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SUMMARY IN ESTONIAN

Viimastel aastakümnetel pööratakse metsanduses majandusliku tasuvuse kõrval tähelepanu ka säästlikule majandamisele, lähtudes metsa teistest väärtustest, sealhulgas elustikulise mitmekesisuse säilitamisest. Üheks vastavaks rakenduseks on elavate ja surnud puude säilitamine lageraiel, millega püütakse jäljendada looduslike häiringute (metsapõlengud, tormikahjustused) käigus alles jäävaid puid. Säilitatavate puude looduskaitselised eesmärgid on: 1) aidata organismidel üle elada periood järgmise metsapõlvkonna tekkeni, 2) pakkuda spetsiifilisi elupaiku metsaliikidele järgmises metsapõlvkonnas ja häiringuliikidele raiesmikel, 3) suurendada liikide levimisvõimalusi maastikul. Raiel elustiku jaoks säilitatavate elusate puude kohta kasutatakse järgnevas terminit „säilikpuu", mis ei ole küll kooskõlas Eesti õigusaktidega, kuid vastab mujal maailmas levinud terminoloogiale.

Käesolev töö annab ülevaate senistest uurimustest säilikpuude eesmärkide kaupa ja neid mõjutavatest tunnustest, toob välja problemaatilised ja väheuuritud valdkonnad (**I**) ning täidab ilmnenud teadmistelünki originaaluuringutega (**II–IV**).

Kokkuvõtteartiklis Euroopa ja Põhja-Ameerika 214 uurimusest säilikpuude mõju kohta elustikule (**I**) leiti valdkondade ebaühtlane kaetus: suurem osa pärineb Põhja-Ameerikast, enamus uurivad säilikpuude lühiajalist mõju ja levimisvõimaluste parandamist maastikul pole uuritud. Metaanalüüsis, kus võrreldi lageraie ja säilikpuudega raie mõju elustikule, ei leitud ühegi liigirühma arvukuse ega liigirikkuse vähenemist säilikpuude jätmise tõttu, kõige rohkem kasu puude jätmisest said linnud ja ektomükoriissed seened (**I**).

Säilikpuude jätmine vähendas kokkuvõtteartiklis käsitletud uurimustest 72% juhtudel raie vahetut kahjulikku mõju elustikule. Säilikpuud suurendasid raiejärgset ellujäämust ektomükoriissetel seentel, epifüütsetel samblikel ja väikestel maapinnaloomadel, kõige vähem parandasid nad eluspüsimist sammaldel ja soontaimedel (**I**). Sama kinnitas ka uurimus **II**, kus säilikpuude epifüütsetest samblikest olid kaks aastat pärast raiet kahjustatud keskmiselt 2%, kuid sammaldest 60%. Peaaegu alati parandas säilikpuude jätmine häiringutega kohastunud putukate ja lindude elutingimusi raiesmikel ning uuenenud küpses metsas vanale metsale iseloomulikel liikidel (**I**).

Elustiku säilitamise edukus sõltub olemasolevate uurimuste järgi alati säilikpuu liigist (**I**), ka uurimus **II** leidis, et haab (*Populus tremula* L.) ja saar (*Fraxinus excelsior* L.) säilitavad samblikke paremini kui teised puuliigid. Säilikpuude suurem hulk (tihedus) suurendab 65% varasema uurimuse järgi nende kasu elustikule (**I**), mis käesolevas töös leidis kinnitust kaitsekorralduslikult oluliste linnuliikide (aga mitte linnustiku üldarvukus ja -liigirikkuse) puhul (**III**). Puude ruumilise asetuse mõju pole nii selge, kuigi 50% varasematest uuringutest leidis, et see on elustikule oluline (**I**).

Looduslikke häiringuid jäljendades peaks säilikpuude mõju elustikule sõltuma metsatüübist, mida peetaksegi oluliseks, kuid on vähe uuritud (**I**). Käesolev töö seda ei kinnitanud: kasvukohatüübi ja säilikpuude arvu koosmõju linnustiku arvukusele ja liigirikkusele ei leitud (**III**) ja sagedasema häiringurežiimiga kasvukohatüüpides ei säilinud üksikuna jäetud puud paremini (**IV**). Puude elumust mõjutasid eelkõige puu liik, diameeter, asend raiesmikul, puude tihedus ja avatus (**IV**). Paremini säilisid kõvalehtpuud (*Fraxinus, Ulmus, Quercus, Acer*), puud endiste ja praeguste metsaservade servas, suurema raiejärgse tihedusega raiesmikel ja vähem avatud maastikul. Pehmelehtpuudel (*Tilia, Alnus, Salix*) ja haabadel säilivad paremini suurema diameetriga, kaskedel (*Betula spp.*) väiksema diameetriga puud. Kuue raiejärgse aasta vältel hukkus raiesmikel kokku 35% puudest, kuid aja jooksul suremus vähenes. Prognoosi kohaselt oleks parima stsenaariumi järgi 100 aasta pärast alles 29% säilikpuudest, halvima järgi 9%.

Antud töö põhjal soovitati edaspidiseks kindlale säilikpuude eesmärgile keskenduvaid uuringud just selleks eesmärgiks sobivate liigirühmade kohta. Uuringuid oleks vaja teha maastiku mastaabis ja pikaajalisemana (sealhulgas uue metsapõlve jõudnud säilikpuude kohta) ning võrrelda tuleks looduslikke häiringuid ja puude säilitamist. Praktikas tuleks säilikpuudeks valida kõige tuulekindlamad, arvestades puu liiki ja asendit raiesmikul ning maastikul, samuti kõige jämedamad, et suurendada nende väärtust elustikule. Säilikpuude hulka hektarile tuleks Eestis suurendada, et tagada piisav hulk puid elustiku jaoks nii praegu kui tulevikus.

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I

PUBLICATIONS

ARTICLE IN PRESS

Review

For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects

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Abstract

Green-tree retention cutting (GTR) is a modification of traditional clear-cutting, aimed at better consideration of biodiversity. We reviewed 214 North American and European studies to answer whether, and under which circumstances, GTR meets its objectives: 'lifeboats' species over the regeneration phase, provides microhabitats for old-forest species in re-established forest stands and for disturbance-phase species on the recent cuts, and enhances species' dispersal by increasing landscape connectivity. To answer these questions is complicated, partly because the target taxa differ regionally and due to research biases: 81% of the studies have been carried out in North America, 82% have been short term, and the objective of improving landscape connectivity has not been studied. A meta-analysis of GTR effects on species richness and abundance of different taxa indicated no negative responses, but birds and ectomycorrhizal fungi benefited most. Compared with clear-cutting, GTR lowered the harvest-related loss of populations or individuals in 72% of studies, and it nearly always improved the habitat for disturbance-phase insects and birds on the cuts and for forest species in the regenerated stand. Lifeboating was most successful for ectomycorrhizal fungi, epiphytic lichens and small ground-dwelling animals, and least successful for bryophytes and vascular plants. Retention tree species always contributed to the success of GTR, followed by tree density (65% of cases) and the spatial arrangement of the trees (50%); the influence of forest type is likely, but insufficiently studied. Ectomycorrhizal fungi, epiphytes, birds, and wood-dependent beetles may be suitable indicator taxa for measuring the success of GTR. For future research, we encourage clearly objective oriented studies of relevant taxa, spatially explicit landscape perspectives, and long-term (including retrospective) studies.
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Keywords: Biodiversity; Biological legacies; Disturbance; Forest management; Landscape connectivity; Retention trees

Contents

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1. Introduction

In the last decades, forestry has been increasingly focusing on multiple values instead of timber production only. One of the crucial issues has been the concern about biodiversity—not only in reserves but implicitly in managed forests as well (Bengtsson et al., 2000; Lindenmayer and Franklin, 2002). For the latter, it is not enough to slightly modify the traditional cutting techniques but the whole aim of forestry should be revised: to preserve biodiversity while retaining the economic viability (Franklin et al., 1997). The primary approach for reaching such an aim has been to use silvicultural techniques that imitate natural disturbances (e.g. Hunter, 1993).

Clear-cutting is the dominant cutting technique in many regions of the world, notably in North America and Europe (e.g. Keenan and Kimmins, 1993; Hannerz and Hånell, 1997; Deal et al., 2002). This dominance has been largely based on economic considerations such as cheaper cutting, larger volume of timber, and easier artificial regeneration with economically suitable tree species in cut areas (Keenan and Kimmins, 1993). Yet, though felling all the trees in a forest stand may resemble a natural stand-replacing disturbance (Esseen et al., 1997), profound differences are evident when evaluated more closely (Swanson and Franklin, 1992; Keenan and Kimmins, 1993; Bengtsson et al., 2000; McRae et al., 2001). Perhaps most importantly, many "biological legacies" of the previous forest structure remain in place after fire, windstorm or disease, and the resulting structural complexity plays an important role in forest ecosystem functioning and for biodiversity (Lindenmayer and Franklin, 2002). Thus, the similarity between clear-cutting and natural disturbances could be increased if structural features of old-forests, such as live and dead trees of varying sizes and multiple canopy layers are purposefully retained on cuts (Franklin et al., 1997; Beese et al., 2003). Such practices have gained popularity during the last two decades and their efficacy is an important subject of forest research.

In this review, we focus on the *direct* consequences for biodiversity of leaving live trees on the cut area—a technique most commonly known as 'green-tree retention' (GTR), which forms a part of the 'variable retention' approach (Franklin et al., 1997). In addition to the direct impact, GTR also has more complicated effects, such as producing coarse woody debris in the regenerating stand or complementing other techniques for sustaining biodiversity (e.g. Franklin et al., 1997; Zenner, 2000; Keeton and Franklin, 2005). Research on GTR became systematic in the late 1980s and has now reached a phase of integration. For example, several large-scale field studies have been initiated in North America (Monserud, 2002) and the Fennoscandian experience has been summarized (Vanha-Majamaa and Jalonen, 2001). In this paper, we take a next step and review whether, and under which circumstances, GTR has met its objectives or, at least, whether the answer can be given on the basis of current knowledge. For that, we define the aims and objectives of GTR as follows.

GTR cutting is a disturbance in a dynamic forest landscape (a mosaic of stands), creating habitats for pioneer species and modifying succession patterns afterwards. Therefore, given that the conditions after stand-replacing disturbances differ from those within forest by definition, comparing GTR cuts with forests (as has often been done) is of secondary importance. Instead, the main question is how forest biota survives in the landscape despite or because of such intensive disturbances. Hence, we see the aim of GTR in sustaining the populations or communities, which are lost in the conventional clear-cutting forestry.

We define three main objectives of GTR as listed in Franklin et al. (1997): (1) 'lifeboating' species and processes over the regeneration phase, (2) enriching re-established forest stands with structural features, and (3) enhancing landscape connectivity. Very broadly, from a biodiversity aspect, these objectives refer to the duration of post-cut occupancy by target species: lifeboating (objective 1) means a continuous occupancy of the cut stand, objective (2) reveals the presence of specific microhabitats that can be inhabited after or during some suitable period, and landscape can be considered connected (objective 3) if individuals or propagules can disperse through the GTR areas. Importantly, these objectives could be reached for all organisms only at a very large scale—the biotic richness of forests is huge, and habitat requirements of the species and communities vary widely. Given that such a scale is usually unachievable in case studies and often for forestry planning as well, large-scale knowledge should be used to select target species or community characteristics both for informing management and measuring its success at a local scale. In practice, however, the local targets depend also on knowledge and conservation priorities, which may be inadequate at the large scale after all. Handling all this variety of smaller-scale targets presents a major challenge for any general assessment of GTR success. Therefore, we pay particular attention to the use of target species or variables in the case studies on GTR.

In this paper, we start with an overview of the aspects that GTR studies have covered so far. We then compare the *average* abundance and diversity of biotic communities on GTR cuts and clear-cuts, using meta-analysis. As null-hypotheses, we test whether the effect of retention trees (i) is similar in terms of two biodiversity responses—species richness and abundance, (ii) is similar across taxa; (iii) does not depend on the density and distribution of the trees; (iv) is generally positive as often expected (e.g. Fries et al., 1997). In the third part of the paper,

we review the evidence for GTR success according to its objectives. To evaluate the efficacy of lifeboating (an objective shared with uneven-aged silviculture), the GTR-cut versus forest comparisons have been included. Fourth, we list the silvicultural key factors that cause *variability* in the effects of GTR. Spatial variation is essential for any comprehensive GTR strategy because the intensity and extent of natural stand-replacing disturbances varies a lot (e.g. Bergeron et al., 2002; Angelstam and Kuuluvainen, 2004). Finally, we discuss the implications on the research on and future use of GTR.

2. Materials and methods

2.1. The sample of studies

We searched electronic databases (e.g. SCOPUS, ISI Web of Science, JSTOR, EBSCO Academic Search Premiere) and reference lists for reports and reviews, which had been published from the beginning of 1981 to August 2006, and described situations where (1) trees had been harvested for timber production from at least 1 ha of mature forest, (2) at least four trees ha^{-1}, but no more than 50% of pre-harvest numbers, had been retained solitarily or in up to 1-ha (in four studies: up to 2-ha) patches for any purpose (i.e. not necessarily for long-term maintenance, but the trees were present at the time of the study), and (3) effects of retained trees on biodiversity and the structure of the cut stand (including the condition of retention trees) had been measured. The 50% upper limit of retention is widely used in practice and, for example in Alaska, it is the threshold at which the plant community structure changes significantly (Deal, 2001). Due to presumably strong and non-measurable confounding effects, we omitted all reports on GTR techniques in intensive plantations or forests of non-native tree species, and the retention of strips of trees along waterbodies. We also omitted the few studies describing tree strips between clear-cuts, though these are clearly analogous to group retention; however, the possible age or type differences between the cuts and the specific elongated shape of the tree group made this technique difficult to compare with more traditional ones.

We did not limit the time-scale of the effects, so the studies range from short-term post-cut measurements to long-term predictive models and retrospective studies performed more than 20 years after the GTR. However, geographically the review is restricted to North America and Europe, since we found only three studies from other parts of the world (Australia: Dignan et al., 1998; Asia: Yoshida et al., 2005; South America: Vergara and Schlatter, 2006).

In several experimental studies, the treatments of our interest had been included as controls only (e.g. prescribed burning compared with GTR). Unavoidably, many such studies may have been missed in our keyword-based search from databases. Furthermore, while the majority of peer-reviewed papers are likely to be included, many master's or doctoral theses and project reports and other grey literature were unavailable for us. Given that the reports are of highly variable quality, often preliminary, and their best-quality parts are often published, we

made no effort to find all of them, and we avoided using them as the only supporting evidence for generalizations. When the results were duplicated in different publications, we only used the most elaborated version.

For the meta-analysis and the assessment of biodiversity objectives, we separated the studies directly relevant to biodiversity.

2.2. The meta-analysis

For meta-analysis, we used 39 case studies with paired numerical data relating to biodiversity condition in clear-cuts (0–3 trees ha^{-1}) and GTR cuts 0–17 years after cutting. Altogether, eight species groups (see Appendix A) and four GTR treatments (retention levels) were distinguished: 1, solitary trees (up to 15% of the numbers or basal area of the pre-harvest stock); 2, group-retention (10-tree to 1-ha groups; altogether up to 20%); 3, two-storey retention (16–33%); 4, shelterwood (34–50%). Dependent variables were the treatment differences from clear-cuts in species richness (incl. ectomycorrhizal morphotypes: Dahlberg et al., 2001; Lazaruk et al., 2005), diversity (mostly Shannon and Simpson indices), and abundance (usually number of individuals or cover; once biomass; twice the number of root tips with mycorrhizal fungi present). We were not interested in absolute values (which vary due to local and methodological factors), so the differences were presented as logarithmed ratios (to normalize distributions), R:

$$R = \ln\left(\frac{g}{c}\right)$$

where g is the average value in GTR cut and c is the value in clear-cut. Significant deviation of R from zero thus indicates that GTR is better or worse than clear-cut. Since the relative diversity (R_d) was very closely related to relative species richness (R_r; $r_{18} = 0.94$, $P < 0.001$), and never reported alone, we omitted R_d from final analyses. R_r and relative abundance (R_a) were strongly correlated as well ($r_{40} = 0.86$, $P < 0.001$), but both were explored due to their different ecological meanings. Altogether, 45 estimates of R_r and 72 estimates of R_a were considered, a total of 39 of these were estimated from figures (Appendix A).

We used one-way ANOVA to test for differences in R_r and R_a between species groups and retention levels, including only categories with at least three estimates. Since many combinations had not been studied, it was not possible to use a multivariate design and test for taxon-specific effects of retention levels (interactions). If a study presented data for several subsequent years, we used the average value. For three studies (Lemieux and Lindgren, 2004; Lindo and Visser, 2004; Lazaruk et al., 2005), which gave separate estimates for the open parts of GTR cuts and the tree groups, we calculated weighted means according to the relative areas. The assumptions of normal distribution (Kolmogorov–Smirnov test) and the homogeneity of variances (Levene's test) were checked prior to analyses. The tests were performed with Statistica 6.0

software (StatSoft, 1984–2001). All confidence intervals (CI) given are at 95% probability.

2.3. Assessing the fulfilment of GTR objectives

In general, GTR might be considered a success if pre-defined target taxa, sensitive to conventional clear-cutting, are viable in landscapes managed with GTR cutting. However, since such viability analyses and, in fact, any landscape-scale analyses are absent so far, we could only assess whether retaining live trees on cuts meets its specific objectives better than clear-cutting. For that, we first stratified the studies according to the three biodiversity objectives of GTR, distinguished the cases exploring meaningful target taxa for each objective (see below), and then checked for statistically significant evidence of the superiority of GTR over clear-cutting. Note that, except in a few long-term studies, such "evidence" does not necessarily mean biologically significant improvement, only a potential for that.

In addition to the comparisons of GTR cuts and clear-cuts used in meta-analysis, we included the cases which (i) described the gradient of biodiversity response from retention trees towards open cut or compared it in the tree groups and treeless parts of GTR cuts and (ii) assessed the performance of strictly tree-dwelling species (epiphytes, squirrels, hole-nesting and canopy-dwelling birds) on GTR-cuts (assuming that these species were absent from clear-cuts). To explore long-term structural enrichment, we included 11 studies on remnant trees in the stands re-established after natural disturbances since such trees can be considered analogues of the retention trees (e.g. Zenner et al., 1998) and the specific consequences of natural disturbances were likely to be diminished by that time. The cases where any cuttings were found to have insignificant influence on the measured variables were omitted because there was no target for GTR.

The species groups of interest, and criteria of success for each objective, were defined as follows:

(1) *Lifeboating* (objective 1) is most important for poor dispersers or rarities all of whose local populations need to be preserved. In particular, this meant omission of a large number of short-term studies on birds (also most mammal studies). Although stand-scale persistence may be important for landscape-scale viability of some old-forest or rare avian species (e.g. Conner et al., 1991) or in extremely impoverished landscapes, it is not likely to be generally so (e.g. Angelstam et al., 2004). GTR was classified successful if these target taxa inhabited GTR areas continuously and, even though their numbers or diversity might have been lower there than in forests, they exceeded those in clear-cuts. Failures were the cases when such biodiversity responses did not differ on GTR cuts and clear-cuts.

(2) *Structural enrichment* (objective 2) was expected to support two kinds of species with narrow habitat requirements, so we assessed its success in two parts. (i) For disturbance-phase species, the objective was met if, for some period after the cutting, their numbers or diversity in GTR cuts exceeded that in both forests and clear-cuts. The objective

was not met if such species were similarly or more abundant in clear-cuts. (ii) For forest species, we checked long-term or retrospective studies for whether post-cut stands regenerated after GTR supported them in greater numbers or diversity than the stands originated from clear-cutting. Short-term studies were omitted, though successful life-boating of such specialist species includes provisioning of their habitat as well (but failure of lifeboating does not mean the failure of structural enrichment). On the other hand, the reports of long-term success which we examined may have included lifeboating in the past, but it was impossible to distinguish that effect due to the absence of continuous monitoring. We omitted the studies on ground vegetation and mycorrhizal fungi, which depend more on soil characteristics, habitat continuity (lifeboating) and adjacent source populations (incl. seed bank) than the GTR-related appearance of specific microhabitats and woody substrata (e.g. Humphrey et al., 2004). An assessment was also impossible for saproxylic insects or their predators, because GTR has often been mixed with the simultaneous retention of dead wood, so the contribution of the live trees remains unclear.

(3) *Improved landscape connectivity* (objective 3) assumes that the species or individuals, which would have become isolated in forest fragments between clear-cuts, are able to disperse through the GTR areas. The obvious targets for the latter are mobile animals with large home-ranges or the species with unstable local populations, which exhibit extinction-immigration dynamics.

3. Results

3.1. The state of ecological research on GTR

Altogether, 214 studies on biodiversity or other ecological effects of GTR were found: 181 papers in peer-reviewed journals, 26 project reports or conference proceedings and seven dissertations. The full list of papers is available upon request from the authors. The average annual number of publications has risen from 0.5 in 1981–1991 to 23.8 in 2001–2005 (Fig. 1) with a steep increase in 1997. As several studies
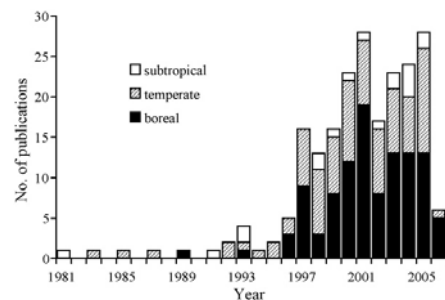

Fig. 1. Distribution of 214 studies on the ecological effects of GTR according to publishing year and study region, 1981–2006.

Table 1
Numbers of GTR studies according to main issues, objects and geographical region (A, North America; E, Europe)

Study issues and objects	Boreal[a]		Temperate[a]		Subtropical[a]	Total
	A	E	A	E	A	
Biodiversity effects[b]	49	22	60	3	10	144 (28)
Epiphytes	1	4	4	1		10 (3)
Ground vegetation	7	6	12			25 (5)
Ectomycorrhizal fungi	5	1	5			11 (2)
Arthropods	5	11	3		1	20 (2)
Amphibians and reptiles			6		1	7
Birds	22		19	2	5	48 (10)
Mammals	9		11		3	23 (6)
Effects on retention trees and regeneration	38	16	45	2	8	109 (28)
Stand regeneration	13	6	18	2	5	44 (13)
Growth of retention trees	3	2	12		2	19 (10)
Stand structure[c]	4	5	5			14 (5)
Wind-resistance	15	2	3			20
Logging damage on trees and soil	3	1	7		1	12
Other ecological and biological effects[d]	10	4	5		1	20
Total	97	42	110	5	19	273 (56)

In brackets—long-term studies (at least 20 years post-cut).
[a] Region.
[b] Incl. five studies on bird nest predation and two on mammal diets (all in North America).
[c] Incl. three studies on GTR as a source of coarse woody debris (all in boreal Europe).
[d] Incl. six studies on the production, germination, dispersal or predation of tree seeds; four studies on GTR effects to genetic structure of regeneration; five studies on the changes in microclimate and five on the changes in soils.

considered more than one large taxon or aspect, a total of 273 general conclusions on GTR effects were distinguished (Table 1).

The research on GTR has been strongly biased in many respects. Eighty-one percent of the studies have been carried out in North America (particularly in the west), including all subtropical studies and most work on temperate forests and on boreal forest vertebrates (Table 1). Though several papers speculate about the possible landscape-scale biodiversity effects of GTR (e.g. Hansen et al., 1995; Taulman et al., 1998), we only found one explicit study on this (Phillips and Hall, 2000). Even the large-scale initiatives in Canada and the western United States (Beese and Bryant, 1999; Aubry et al., 2004; Serrouya and D'Eon, 2004) actually collected and analyzed stand-scale data. The situation regarding time-span is slightly better: 39 studies (18%) with 56 conclusions covered at least 20 years after the cut, while 82% of the studies were only short term (Table 1). Of the three objectives of GTR, mostly short-term lifeboating (54% of the 214 studies) has been studied, and even this is usually for common mobile species at small scales. The long-term effects of structural enrichment have been explored considerably less often (13%), and we did not find any studies on improving the landscape connectivity with live retention trees.

3.2. Meta-analysis of general effects

The effect of GTR (compared with clear-cutting; R) differed between the major taxa studied both when measured as a change in average species-richness ($F_{5,38} = 4.8$; $P = 0.0017$)

or abundance ($F_{5,56} = 4.1$; $P = 0.003$). No species group responded negatively, while the species richness and abundance of birds and ectomycorrhizal fungi as well as the abundance of woody plants increased significantly (Fig. 2). These latter increases differed from the weak negative tendencies in herbs and grasses (Tukey's HSD tests: $P = 0.006–0.019$; for fungal species richness, $P = 0.098$, for fungal abundance, $P = 0.062$).
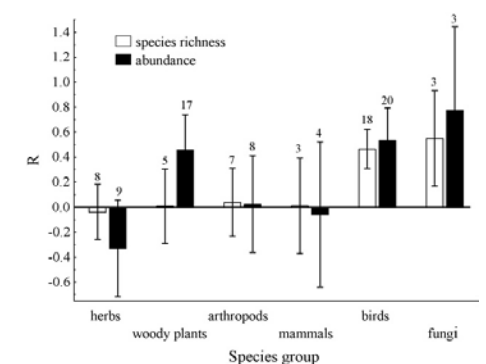

Fig. 2. Mean differences between GTR-cuts and clear-cuts in the species richness and abundance of different species groups. R, natural logarithm of ratio of the values in GTR-cuts vs. clear-cuts (positive values indicate higher values in GTR cuts); labels indicate the number of studies; lines are 95% confidence intervals for the mean.
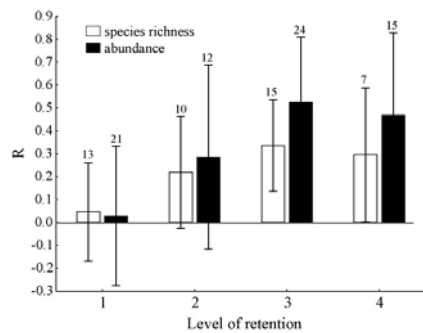
Fig. 3. Mean differences between GTR-cuts and clear-cuts in species richness and abundance of eight taxa in relation to retention levels: 1, solitary trees; 2, group-retention; 3, two-storey retention; 4, shelterwood. R, natural logarithm of ratio of the values in GTR-cuts vs. clear-cuts (positive values indicate higher values in GTR cuts); labels indicate the number of studies; lines are 95% confidence intervals for the mean. See Appendix A for the taxa included.

No retention level was worse than clear-cutting, and significant positive effects of GTR appeared for the highest levels of retention (two-storey retention and shelterwood), i.e. retaining of more than 15% of the growing stock (Fig. 3). However, we were not able to demonstrate statistically significant differences of R between retention levels for species richness ($F_{3,41} = 1.4$; $P = 0.245$) or abundance ($F_{3,64} = 1.7$; $P = 0.185$).

3.3. The lifeboating objective

Of the species groups studied, we considered lifeboating generally relevant for cryptogams, plants, arthropods, and small ground-dwelling vertebrates, which had been the focus of 71% of the studies exploring this objective. Statistically significant improvements in the survival of their populations or individuals after GTR, compared with clear-cutting, were reported in 72% of the 57 studies (Table 2). The effectiveness depended on taxon (see also Maguire et al., 2005; Lõhmus et al., 2006): it was best for ectomycorrhizal fungi, epiphytic lichens and small ground-dwelling animals such as carabid beetles, salamanders, and the vole *Clethrionomys gapperi*. In contrast, GTR was usually insufficient to conserve forest bryophytes (both epiphytic and epigeic species) and vascular plants (Table 2). Though increased density of trees reduces microclimatic changes and enhances bryophyte survival (Hannerz and Hånell, 1997; Beese and Bryant, 1999; Nelson and Halpern, 2005), most sensitive and rare taxa, such as liverworts, still disappeared (Nelson and Halpern, 2005). Also, only a few species of forest-interior saproxylic beetles occupied GTR areas even at high levels of retention (Serrouya and D'Eon, 2004), though these may still include some threatened species that are lost after clear-cutting (Martikainen, 2001; Hyvärinen et al., 2005).

Even for the best surviving taxa, some logging-related damage is unavoidable (e.g. for lichens: Hedenås and Ericson, 2003; Coxson and Stevenson, 2005; Lõhmus et al., 2006) and, given that most studies had explored only short-term effects, the

final success rates of lifeboating may also be overestimated here. For example, the logging-related decline of *Clethrionomys gapperi* is delayed by 1–3 years (Fisher and Wilkinson, 2005). Yet, the improved short-term survival obviously contributes to long-term persistence. Notably, populations of mature-forest ectomycorrhizal fungi, which survive on the roots of large live retention trees, can inhabit the roots of adjacent seedlings (Kranabetter, 1999; Cline et al., 2005), and residual trees obviously become dispersal centres for lichens as indicated by their diversity (particularly of alectorioid and cyanobacterial species) near large remnant trees in forests regenerated after cuttings or fire (Neitlich and McCune, 1997; Peck and McCune, 1997; Sillett and Goslin, 1999). In addition, lifeboating of these taxa may have cascade effects in the GTR areas. Several mammal species use the epiphytes or fruit-bodies of fungi (and, in turn, may disperse these) for food, while a significant part of soil fauna depends on ectomycorrhizal fungi (Hayward et al., 1999; Carey et al., 2002; Luoma et al., 2004; Fisher and Wilkinson, 2005); changes in invertebrate biomass caused by silvicultural practices may influence the breeding success of passerine birds (Duguay et al., 2000).

3.4. The structural enrichment objective

For disturbance-phase species, retention trees improved the cut areas in 76% of the 37 case studies: seldom for mammals, but always for insects and usually for birds (Table 2). Notably, in six studies out of eight found, the threatened Olive-sided Flycatcher (*Contopus cooperi*) preferred GTR cuts to both forest and clear-cuts (e.g. Lance and Phinney, 2001; Chan-McLeod and Bunnell, 2002). Also, a few raptor and woodpecker species preferred to nest on retention trees on cuts, probably due to lower risk of nest predation or favourable foraging conditions around (Sonerud, 1985; Niemi and Hanowski, 1997; Rolstad et al., 2000).

For forest species, the GTR-induced structural effects could be mostly derived from circumstantial evidence: at least 77 cases have described the features of re-establishing stands (incl. characteristics of retention trees; Table 1) and there is a large body of literature on stand-scale habitat requirements of forest biota. For example, the mixture of woody species in the future stand, which greatly influences biodiversity in general, is strongly related to the level of green-tree retention (Hansen et al., 1995; Rose and Muir, 1997; Deal and Tappeiner, 2002; Deal et al., 2002). However, only 24 long-term or retrospective records linked the stand structure to the biodiversity response directly; of these, 13 of 14 results (93%) on relevant taxa detected significant benefit from GTR (Table 2). Hence, for many forest species – even though they could not be continuously maintained – tree retention obviously increases occupancy time in regenerating stands, which is particularly important in short-rotation forestry (e.g. Mazurek and Zielinski, 2004). For example, the abundance of late-seral birds in GTR stands is likely to exceed that in clear-cut stands during the period between canopy closing and about 100 post-cut years (Hansen et al.,

1995). In timber-harvesting areas, some threatened bird species, such as spotted owl (*Strix occidentalis*) or red-cockaded woodpecker (*Picoides borealis*) in North America, may in fact be viable only if residual trees are available for their nesting or foraging (e.g. Franklin et al., 1997; Phillips and Hall, 2000).

Obviously the main effect of structural enrichment is due to the use of retention trees as substrata or microhabitats, but the changed canopy or vegetation structure around the trees may have some importance as well. For example, medium-sized forest-dwelling raptors nested in hemiboreal forest stands younger than 80 years only if older trees were present for nest-building. However, after taking into account tree size, forest type and landscape characteristics, the birds still strongly preferred stands with old-growth features (Lõhmus, 2005, 2006).

3.5. Technical considerations for successful GTR

It has been argued repeatedly that the efficacy of GTR depends on geographical location and climate (e.g. Valkonen et al., 2002; Hedenås and Ericson, 2003; Klenner and Sullivan, 2003), but our review found that no study has explored these effects so far. For disturbance-phase species, even smaller-scale requirements of GTR are unclear because silvicultural studies have not distinguished these taxa. For forest species, four technical aspects could be summarized (Table 2). Among these, retention tree species was always a significant factor and thus should be of primary concern, followed by tree density (statistically significant in 65% of cases). Yet, the tree species effects were mostly obtained from comparisons of stands of different tree species; only two studies compared different tree species on the same cuts (Kranabetter and Kroger, 2001; Lõhmus et al., 2006). The spatial arrangement of the trees had less importance (50%) on forest biodiversity, and the influence of forest type – although central for the disturbance-mimicking paradigm (Fries et al., 1997) – has remained nearly unexplored according to our review.

The post-cut survival of various forest taxa is positively related to the density of trees retained (e.g. Ross et al., 2000; Lazaruk et al., 2005; Halpern et al., 2005), though the relationship is not necessarily linear (Serrouya and D'Eon, 2004; Luoma et al., 2004; Harrison et al., 2005). For ground-dwelling bryophytes, late-seral vascular plants and flying squirrels, the retention of less than 20% of the growing stock does not differ much from clear-cutting, while shelterwood stands resembled forests (Hannerz and Hånell, 1993, 1997; Taulman et al., 1998; Beese and Bryant, 1999; Jalonen and Vanha-Majamaa, 2001; Sullivan and Sullivan, 2001; Bradbury, 2004; Halpern et al., 2005). For vertebrates of conservation concern, the minimum required basal areas for GTR was 9–15 m²/ha (Conner et al., 1991; Ross et al., 2000).

There is no straightforward answer as to whether the retention trees should be aggregated or dispersed, partly because the tree groups are smaller than required for retaining forest-interior conditions anyway (at least 1 ha; Koivula, 2002)

Table 2
General fulfilment of the objectives of GTR, and its dependence on four silvicultural considerations according to 183 case studies

Species group[a]	General[b]			Tree density[b,c]		Tree grouping[b]		Tree species[b]		Site type[b]
	S	D	L	S	L	S	L	S	L	S
Epiphytes										
Lichens (A)	5/2		3/0	0[1]/0		1/0		1/0	0[1]/0	0[1]/0
Bryophytes (A)	0/2					0/1		1/0		
Ground vegetation										
Bryophytes (B)	6/3		0/1	1/1		0/2				
Herbs, grasses (B)	6/5	2/2	0/3		1/0	1/2		1/0		0[3]/0
Woody plants (B)	4/2	2/3	3/2	2/2	1/0			2/0		
Mycorrhizal fungi (B)	7/0		1/0	1/1		0/2		1/0		0[2]/0
Arthropods (A)	6/1	7/0	2/0	3/1		1/3		2[1]/0		1[2]/0
Salamanders (A)	4/1			2/2		0/1		1/0		
Birds (C)	22/3	20/5	5/1	10/2	4/0	3/2	1/0	6[2]/0	3/0	
Mammals										
Ground-dwellers (A)	3/0	1/3	1/0	1/0		2/0				
Squirrels (C)	1/0		1/0	1/0				1/0		
Bats (C)	3/0	0/1	1/0	0/2		0/1		1/1		
Total[d]	41/16	28/9	13/1	10[1]/7	4/0	5/11	1/0	9[1]/0	3[1]/0	1[8]/0

The objectives: S, short-term lifeboating of forest species; L, long-term structural enrichment; D, short-term structural enrichment for disturbance-phase species. The numbers are statistically significant/non-significant cases; additional studies that referred to some effects, but did not demonstrate them, are indicated in superscript.
[a] Species groups have been roughly divided into those requiring both lifeboating and structural enrichment of the future stand (A), mostly lifeboating (B) or mostly structural enrichment (C).
[b] No. of statistically significant/non-significant effects.
[c] Only dispersed retention considered.
[d] Only the species groups relevant for each objective considered.

and in fine-grained clear-cutting systems such groups are treated as separate stands rather than retention trees. Currently, there is more evidence in favour of patchy retention: positive effects of aggregation have been repeatedly noticed (Table 2) and only two studies have considered it microclimatically less favourable (for epiphytes—Peck and McCune, 1997; but see Hazell and Gustafsson, 1999 for an opposite view; for ectomycorrhizal fungi—Luoma et al., 2004). It must be remembered, however, that at a fixed retention level, dispersed trees might promote dispersal of many organisms (such as cryptogams or invertebrates). For example, being sources of inocula for multi-stage and late-stage fungi (Kranabetter, 1999), retention trees might be more effective if they are dispersed, given the short dispersal distances of mycorrhiza (Hagerman et al., 1999; Lazaruk et al., 2005). Yet, our review shows that this aspect (objective 3 of GTR) has not been tested yet.

Fragmented and circumstantial evidence indicates that the success of GTR may differ along moisture, and perhaps also soil fertility, gradients, although no study has addressed this comprehensively so far. Moisture-dependent responses to GTR have been demonstrated for carabid beetles (Koivula, 2002), and three studies have attributed the weakness of the response in ground beetle and ectomycorrhizal fungus communities to moist conditions (Kranabetter and Kroger, 2001; Lemieux and Lindgren, 2004; Luoma et al., 2004). Plant cover develops differently depending on soil fertility levels after harvesting (Jalonen and Vanha-Majamaa, 2001; Bradbury, 2004; Halpern et al., 2005), and these differences are likely to change habitat suitability for other species requiring the retention trees (e.g. Kuuluvainen and Pukkala, 1989; Jakobsson and Elfving, 2004).

4. Discussion

The review of literature revealed three practical issues of the biodiversity aspects of GTR: (1) differential responses among species groups (implications for value setting and monitoring), (2) large-scale resemblance to stand-replacing disturbances (implications for landscape planning), and (3) direct effects of different characteristics of retention trees (stand-scale silvicultural considerations).

4.1. Taxon-specific responses to GTR, and the target taxa

Compared with clear-cutting, GTR appeared to improve the habitat to differing extent, and by various pathways, for different taxa, but it had limited or no negative impact in terms of species richness and abundance. Among the species groups covered in the meta-analysis, only the cover of grasses and herbs tended to be somewhat smaller in the presence of trees (Fig. 2; see also Hannerz and Hånell, 1997). However, that decrease is mostly due to the reduced invasion of pioneer species and, given that forest species survive better (Hannerz and Hånell, 1997; Beese and Bryant, 1999), total species richness did not decrease significantly. Other evidence of a negative effect resulting from GTR is restricted

to the decreased abundance of some open-land birds (e.g. Annand and Thompson, 1997; King and DeGraaf, 2000), rodents (e.g. Moses and Boutin, 2001; Sullivan and Sullivan, 2001) and the regeneration of light-demanding tree species (Holgen and Hånell, 2000; Brais et al., 2004; Oliver et al., 2005). Importantly, the species preferring clear-cuts to GTR-cuts are mostly common meadow- or wetland-dwelling species (e.g. Hannerz and Hånell, 1993; Lance and Phinney, 2001; Moses and Boutin, 2001), whose populations in forest lands are probably marginal. Moreover, GTR seems to be flexible enough to provide openings (e.g. between tree-groups) for such species if needed (Franklin et al., 1997).

The taxon specificity of GTR effects has important implications for research and practical forest management. We suggest that the taxa that respond most clearly are suitable for monitoring forest management, i.e. comparing different GTR techniques and assessing the general state of biodiversity considerations in silviculture. In contrast, the management-sensitive taxa, whose performance has not been improved with GTR, are the clearest research priorities regarding their viability and further modifications of management techniques to enhance it.

So far, the selection of study taxon has been rather random and, considering the objectives of GTR, often not indicative or even relevant for the treatment. For example, 29% of case studies on pre- versus post-cut occupancy of forest stands were about birds (Table 2), and short-term benefits of GTR were very clear for them indeed. However, given their good dispersal abilities, birds (notably the non-threatened species) may not require the continuous occupation of particular stands if suitable stands are developing at the same rate as they are being cut in the surroundings. Thus, landscape-scale planning of cuttings and the resulting mosaic of stands in different succession phases is obviously much more relevant for birds (Welsh, 1987; Angelstam et al., 2004). For them, the main role of GTR could be its potential to create suitable stand structures in post-cut areas, notably the old-growth features in young forests, which would extend the duration of suitable phase in stands managed on a rotational basis. Thus bird communities in landscape mosaics and young stands could be very indicative for forestry. However, the long-term structural effects were actually the least explored in avian studies, and the landscape perspective has not been investigated at all.

In contrast to birds, ectomycorrhizal fungi – the other species group for which GTR seemed to be highly beneficial according to our meta-analysis – obviously depended strongly on lifeboating. In addition to these fungi, lifeboating success could be assessed using epiphytes, which were not included in our meta-analysis because clear-cuts do not have high-quality substrata on them at all. However, the long-term effect of GTR for epiphytes is insufficiently studied so far. At least bryophytes – poorly surviving on the cuts in the short term – are obviously able to re-occupy young stands in the presence of substrata and source populations nearby (Lõhmus and Lõhmus, in press). Hence, for them, lifeboating

may be less important than the structural enrichment of the future stands.

In the meta-analysis, we found no general effect of GTR on arthropods, which may be due to the pooling of arthropod taxa having different responses (see Serrouya and D'Eon, 2004). Wood-depending beetles probably benefit most due to the structural enrichment, and the disturbance-phase species are indeed among the clearest candidates for guiding the management towards this objective. However, this effect may be mostly indirect and delayed, since many such threatened species depend on large-dimension dead wood, which will be created along with the death of the live trees on the cuts. The same is true for threatened polypore fungi (Junninen et al., 2007).

4.2. Retention trees in the context of natural disturbances

To create post-cut habitats more suitable for forest biodiversity, cuttings should resemble natural disturbance regimes, such as fire (Hunter, 1993; Steventon et al., 1998). As discussed above, GTR is clearly more favourable in this respect, but two questions remain: does GTR mimic the disturbances well enough, and where should it be used?

Within the GTR framework of objectives, we suggest that: (i) GTR is likely to retain forest species better than fire; (ii) GTR alone cannot provide all the fire-created structures for disturbance-phase species (Dahlberg et al., 2001; Hyvärinen et al., 2005; Bradbury, 2006), though it may create woody substrata for thermophilous species (Martikainen, 2001); (iii) GTR may be equal to fire regarding long-term structural enrichment, at least the provision of old live trees. For example, fire modifies the communities of beetles (Wikars and Schimmel, 2001; Hyvärinen et al., 2005) and ectomycorrhizal fungi (Dahlberg et al., 2001; Lazaruk et al., 2005) much more that any cutting. Also the composition of bird fauna (Hobson and Schieck, 1999; Stuart-Smith et al., 2006) or plant cover (Haeussler and Bergeron, 2004) often differ after fire and cuttings. Due to such deviations, many studies suggest the use of a variety of silvicultural techniques to provide suitable conditions to different taxa (Annand and Thompson, 1997; Taulman et al., 1998; Steventon et al., 1998; Carey, 2000; King and DeGraaf, 2000; Patriquin and Barclay, 2003); this also includes the protection of old-growth patches for the most sensitive species (Rosso et al., 2000; Keon and Muir, 2002). We are, however, not aware of any data-based synthesis of these options (considering also the taxon specificity discussed above) to judge which additional management techniques should complement GTR, and to what extent. Thus, the existing prescriptions for GTR planning are still very general, basically distinguishing only the strategies in homogeneous and heterogeneous landscapes.

In homogeneous landscapes, region-specific average characteristics (frequency, severity) of natural disturbances, and the trees surviving in these, could be used as a starting point for planning GTR. For example, the highest structural complexity of stands in the Pacific Northwest could be achieved by retaining 10–40 trees ha^{-1}, which corresponds to the average number of remnant trees in old-growth forests (Hansen et al.,

1995; Zenner, 2000). Any average level does not mean, however, that the trees should be equally dispersed: instead, various local densities and mixtures of solitary trees, tree-groups, and gaps are likely to meet the need of different taxa best (Traut and Muir, 2000; Sullivan and Sullivan, 2001; Luoma et al., 2004; Stuart-Smith et al., 2006). Moreover, though conceptually the optimal retention levels are easy to imagine – they should sustain most forest species and satisfy the human need for timber as well – determining what such optima might be in practice may be complicated. Thus, guidelines based on natural remnant trees should address the post-cut mortality of trees and increase the initial retention densities, whereas economic yield calculations may suggest an opposite need. For example, Hansen et al. (1995) report for the Pacific Northwest that in case of five large trees ha^{-1} many bird species are retained and economic yield does not decrease significantly. Also, the growth rate of the regeneration of light-demanding tree species decreases rapidly when the density of large retention trees exceeds 15 per hectare (e.g. Rose and Muir, 1997; Zenner et al., 1998). In areas historically dominated by disturbance-adapted tree species, GTR may even suppress their regeneration to such an extent that the retention of none or only a few trees has been recommended (Oliver et al., 2005). On the other hand, our meta-analysis indicated that GTR can also enhance the abundance of tree-seedlings significantly; this effect resulted obviously because the focus of these studies was on shade-tolerant tree species.

Heterogeneous landscapes, where topography and water regime have created a mosaic of patches with different disturbance regimes, would require a spatially explicit planning of cutting methods and GTR levels (McRae et al., 2001; Keeton and Franklin, 2004). For example, in the generally dry boreal landscapes, it has been proposed that tree groups should be left in the wet-forest and forested-peatland patches, which support high vegetation diversity (Vanha-Majamaa and Jalonen, 2001). In Sweden, Fries et al. (1997) suggest a gradient of 5–20 pines ha^{-1} in dry pine sites, variable patterns of dispersed and patchy retention in mesic successional forests to selection systems or shelterwood retaining one-third of the trees in moist spruce stands. Yet, testing the effectiveness of such mosaic solutions, and adapting them further to the needs of biodiversity, remains a global challenge. Even carefully designed spatially explicit management systems have created landscapes structurally very different from naturally developing ones (Cissel et al., 1998, 1999), so the primary question is which deviations are still within the limits of tolerance for most of native biota.

4.3. Stand-scale management

Among the reviewed studies, tree species appeared to be the most influential technical consideration for biodiversity. Theoretically, as different tree species host different biotic communities, there can be no universal prioritization for retention (all native tree species should be represented at the landscape-scale). However, two complementary preferences for practical use emerged (e.g. Lõhmus et al., 2006): (1) rare

tree species hosting threatened biotic communities, or those with particular qualities not found in the other tree species in that landscape and (2) tree species with high future value for biodiversity, resulting from low mortality and quick development of important features on GTR-cuts (note the 38 studies exploring growth or wind-resistance of retention trees; Table 1). For example, large aspens (*Populus* spp.) or hardwoods with coarse bark are priority trees for conserving epiphytic lichens in boreal and temperate landscapes (Hazell et al., 1998; McGee and Kimmerer, 2002).

The selection of live cavity-trees, which are preferred by hole-nesters and persist much better than cavities in snags (Remm et al., 2006), is more complicated. Though hollow oaks (*Quercus* spp.) and other hardwoods could be superb nest sites (Chambers et al., 1997; Taulman et al., 1998), the quickly growing aspens may be the only cavity-trees left in managed boreal forests (Sandström, 1992). Here, a long-term strategy could include both the preservation of existing values (hollow aspens) and the creation of new options (intact hardwoods where cavities will be formed in the future). Finally, other silvicultural techniques than GTR (notably uneven-aged systems) should be considered for the tree species with high biodiversity value in the forest, but poor survival on GTR-cuts (e.g. old spruces, *Picea* spp.; Fries et al., 1997; Lõhmus, 2006).

A crucial point regarding the selection of retention trees is that the characteristics other than species (such as age, size or shape of the crown) have received almost no attention. Thus, since there are no specific requirements for the trees retained for biodiversity purposes, it was not possible to distinguish between GTR, shelterwood, and seed tree cutting in most of the studies reporting <50% retention levels. Therefore, on the one hand, the potential of GTR to support biodiversity may be higher than reported here. At the same time, however, there may be 'internal resources' in GTR: for example, in Estonia (hemiboreal Europe) only 37% of all trees in the GTR cuts exceeded 30 cm diameter at breast height, and for some species (such as *Fraxinus excelsior* or *Tilia cordata*) this share was as low as 10–15% (Rosenvald and Lõhmus, 2005). These small and young trees have hardly any importance for lifeboating of, for example, epiphytes (Lõhmus et al., 2006), and their role for structural enrichment will realize only after a long time.

The optimum density and spatial configuration of retention trees have been listed among the most important questions for retention-harvest research (Franklin et al., 1997). No general answer has been provided so far, and our meta-analysis confirms the lack of such research. The weakness of retention level effects was most likely due to the wide variation that resulted from the pooling of different taxa. Hence, the stand-scale optimum is still a question of values (target taxa), which again points to the need to vary retention levels across landscape for multiple targets. Also the effect of spatial configuration of the trees was not clear in either our meta-analysis or collating individual studies. Though grouping of trees seems to benefit a larger number of taxa, dispersed retention may be more appropriate for dispersal and for certain species groups. Here, the current knowledge is still in the stage of theoretical comparison as presented by Franklin et al. (1997).

5. Conclusions: research needs

We conclude that despite extensive efforts in the last decade to study the consequences of GTR for biodiversity, at least three major improvements are necessary to test and ultimately increase the efficacy of this silvicultural technique.

(1) The studies should specify the particular objective of the GTR explored and, thereby, have a clear ecological reasoning for the selection of study taxa. In particular, it is unknown to what extent retention trees improve the landscape connectivity (i.e. dispersal) for relevant species groups (e.g. mobile animals with large home-ranges or the species with pronounced extinction-immigration dynamics). Also, there is a shortage of short-term (lifeboating) studies on poor dispersers and disturbance-phase species.
(2) Spatially explicit landscape perspectives on GTR as a biodiversity-protection tool are urgently needed, particularly with regard to (1) the viability of threatened species, which at the scale of individual cuts are so rare that statistical power to detect any effects has been extremely low and (2) applying varying retention levels in heterogeneous landscapes according to presumable disturbance regimes in different site-types, and comparing the biodiversity effects with fixed-level retention. Additionally, the effects of GTR should be compared in forest landscapes that have different histories. For example, the biodiversity values, and consequently the rationale for the use of GTR, may be very different in semi-natural forests, with a management history of only a century, compared with long-term agricultural areas currently afforested using exotic plantations.
(3) There is a need to extend the time-scale of studies, particularly to assess the objective of long-term structural enrichment. In dynamic landscapes, the latter may be more crucial than temporary lifeboating for long-term survival of forest biota. In addition to the few pioneering projects in the western United States and Canada (Monserud, 2002), long-term studies are needed in other forest regions and continents. We also encourage retrospective conservation research in areas where ancient trees, comparable to the present-day retention trees, have been protected in managed forests for a long time.

Appendix A

Data for the meta-analysis: relative differences (*R*) between GTR cuts and clear-cuts in the abundance and species richness of eight species groups as calculated from 39 publications.

Species group	R		Retention level[a]	Years post-cut	Retained tree species[b]	Region[c]	Source[d]
	Abundance	Species richness					
Herbs	−1.007		1	3	C	AT	3
	−0.262		3	3	C	AT	3
		−0.187	3	1	D	AS	11
		−0.112	4	1	D	AS	11
	−0.550	−0.028	3	5	C	EB	12
	−0.235	0.015	1	1	D	AT	17
	−0.070	0.048	3	1	D	AT	17
	−0.834	−0.183	4	1	D	AT	17
	−0.402	−0.067	4	1	D	AT	17
	0.375		2	1	C	EB	19
		0.245	1	1.5	C	AT	30
	0.019	−0.085	1	17	C	AB	38
Bryophytes	0.223		1	3	C	AT	3
	2.303		3	3	C	AT	3
	0.934		3	7–8	C	EB	13
	0.206	−0.039	2	1	C	EB	19
	−0.221		1	17	C	AB	38
Woody plants	1.872		4	6	D	ET	1
	2.079		5	6	D	ET	1
	0.423		1	2	D	AT	2
	0.290		3	2	D	AT	2
	0.693		1	3	C	AT	3
	1.735		3	3	C	AT	3
	−0.486		4	1–2	D	AB	4
	0.080		3	1	D	AS	11
	0.118		4	1	D	AS	11
	0.290		5	9–11	C	EB	16
	−0.077	0.039	1	1	D	AT	17
	−0.206	0.031	3	1	D	AT	17
	−0.261	−0.016	4	1	D	AT	17
	1.459		5	6	C	ET	29
		0.167	1	1.5	C	AT	30
	0.123		3	1	D	AS	32
	0.170		4	1	D	AS	32
	−0.491	−0.182	1	17	C	AB	38
Arthropods	0.745		1	15	D	AT	9
	−1.099	−0.476	1	1	C	EB	18
	0.288	0.723	3	1	C	EB	18
	−0.011	−0.154	2	1	C	EB	21
	0.282	0.251	2	2–4	C	AB	24
	−0.288		4	2.5	D	AB	26
	0.537		4	2.5	C	AB	26
	−0.072	−0.010	2	1–3	C	EB	34
	−0.156	−0.095	2	1–2	C	EB	35
Salamanders	1.386		3	1	D	AS	11
	2.079		4	1	D	AS	11
	−0.636		1	1–4	D	AT	14
	−0.435		3	1–4	D	AT	14
	0.009		4	1–4	D	AT	14
Small mammals	−0.037		3	1–2	C	AB	36
	−0.189	−0.025	1	1–4	C	AB	37
	−0.047	−0.034	2	1–4	C	AB	37
	0.034	0.089	1	17	C	AB	38

Appendix A (Continued)

Species group	R		Retention level[a]	Years post-cut	Retained tree species[b]	Region[c]	Source[d]
	Abundance	Species richness					
Birds	−0.033	0.056	1	2	D	AT	2
	−0.033	0.000	3	2	D	AT	2
	0.693	0.134	1	3	C	AT	3
	0.725	0.452	3	3	C	AT	3
	0.126	0.231	3	2	CD	AB	5
	0.334	0.251	3	2	CD	AB	6
	0.574	0.441	1	1	C	AB	7
	0.418	0.611	3	1	C	AB	7
	0.146		1	10–15	D	AT	10
	1.041	0.924	2	2	D	AS	15
		0.314	4	3–5	D	AT	20
	0.565	0.661	3	1–3	C	AB	22
	1.435	1.329	3	1	D	AS	25
	1.569	1.329	4	1	D	AS	25
	0.835	0.611	2	1	C	AT	27
	0.029	0.234	2	3–9	D	AT	28
	0.472		1	2	CD	AB	31
	0.784		2	2	CD	AB	31
	0.234		1	15	CD	AB	31
	0.166		2	15	CD	AB	31
		0.511	2	10	C	AB	33
	0.593	−0.105	3	1–2	C	AB	36
		0.366	3	2–6	C	AT	39
Ectomycorrhizal fungi	0.336	0.182	1	0.5	C	EB	8
	0.989	0.663	3	2	CD	AB	23
	1.002	0.804	4	2	CD	AB	23

R-values in italics are based on values derived from graphs.

[a] Retention levels: 1, solitary trees; 2, group-retention; 3, two-storey retention (16–33%); 4, shelterwood (34–50%).

[b] Species of retention trees: C, conifers; D, deciduous trees.

[c] Geographical region: A, North America; E, Europe; B, boreal; T, temperate; S, subtropical.

[d] Source: 1, Agestam et al. (2003); 2, Baker and Lacki (1997); 3, Beese and Bryant (1999); 4, Brais et al. (2004); 5, Chambers et al. (1999); 6, Chambers and McComb (1997); 7, Chan-McLeod and Bunnell (2002); 8, Dahlberg et al. (2001); 9, Duguay et al. (2000); 10, Duguay et al. (2001); 11, Felix et al. (2004); 12, Hannerz and Hånell (1993); 13, Hannerz and Hånell (1997); 14, Harpole and Haas (1999); 15, Harrison and Kilgo (2004); 16, Holgen and Hånell (2000); 17, Hood (2001); 18, Hyvärinen et al. (2005); 19, Jalonen and Vanha-Majamaa (2001); 20, King and DeGraaf (2000); 21, Koivula (2002); 22, Lance and Phinney (2001); 23, Lazaruk et al. (2005); 24, Lemieux and Lindgren (2004); 25, Lesak et al. (2004); 26, Lindo and Visser (2004); 27, MacKenzie and Steventon (1996); 28, Merrill et al. (1998); 29, Nilsson et al. (2002); 30, North et al. (1996); 31, Schieck and Hobson (2000); 32, Schweitzer (2004); 33, Seip and Parker (1997); 34, Siira-Pietikäinen et al. (2001); 35, Siira-Pietikäinen et al. (2003); 36, Steventon et al. (1998); 37, Sullivan and Sullivan (2001); 38, Sullivan et al. (2000); 39, Vega (1993).

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Effectiveness of solitary retention trees for conserving epiphytes: differential short-term responses of bryophytes and lichens

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Abstract: Green-tree retention (GTR) on clearcuts is an attempt to mimic natural disturbances and provide habitat for species that are generally absent in clear-cut stands, but its efficacy for sustaining biodiversity is poorly known. We studied (*i*) the total cover and vitality of lichens and bryophytes on four common tree species in three locations (centre and edge of GTR cuts and adjacent forest) and (*ii*) the composition of and damage to various epiphytic species on European aspen (*Populus tremula* L.) and birches (*Betula* spp.) in Estonia during 2 postharvesting years. Bryophytes on all tree species throughout the GTR cuts were severely unhealthy (60% of shoots desiccated, on average); lichens were much more robust (2% of thalli bleached or broken), particularly at the edges of harvested areas and on aspen and European ash (*Fraxinus excelsior* L.; hereinafter referred to as ash). Most lichen damage appeared to be unrelated to logging (the damaged species were also affected in forests). Aspen hosted many more species, including those of conservation concern, than birch. If tree species, size, and bark texture are carefully considered, GTR could be a successful tool for conserving lichens, particularly many microlichens on aspen and ash. However, bryophytes on solitary trees were generally unhealthy, at least in the short term.

Résumé : La conservation d'arbres vivants dans les zones de coupe à blanc est une tentative pour imiter les perturbations naturelles et fournir un habitat pour les espèces qui sont généralement absentes dans les peuplements coupés à blanc, mais son efficacité à maintenir la biodiversité est mal connue. Les auteurs ont étudié (*i*) le couvert total et la vitalité des lichens et des bryophytes sur quatre espèces communes d'arbres dans trois sites (le centre, la bordure des coupes avec réserves et la forêt adjacente) et (*ii*) la composition et les dommages subis par différentes espèces d'épiphytes sur les peupliers (*Populus tremula* L.) et les bouleaux (*Betula* spp.) durant les deux années qui ont suivi la récolte en Estonie. Les bryophytes étaient sévèrement affectées (en moyenne 60 % des pousses étaient desséchées) sur toutes les espèces d'arbres partout dans les coupes avec réserves; les lichens étaient beaucoup plus robustes (2 % des thalles étaient blanchis ou brisés), particulièrement en bordure des zones de récolte et sur les peupliers et les frênes (*Fraxinus excelsior* L.). La plupart des dommages subis par les lichens ne semblaient pas être reliés à la coupe (les espèces endommagées étaient aussi affectées en forêt). Le peuplier hébergeait beaucoup plus d'espèces que le bouleau, incluant celles qui devaient être protégées. Si les espèces d'arbres, la taille et la texture de l'écorce sont soigneusement considérées, la coupe avec réserves pourrait être un outil de conservation efficace pour les lichens, particulièrement pour plusieurs microlichens sur le peuplier et le frêne. Cependant, les bryophytes sur les arbres solitaires étaient généralement en mauvais état, du moins à court terme.

[Traduit par la Rédaction]

Introduction

Green-tree retention (GTR) — leaving large live trees during clear-cutting instead of felling them all — has gained popularity in the management of boreal and temperate forests over the past decade (Angelstam and Pettersson 1997; Lindenmayer and Franklin 2002; Mielikäinen and Hynynen 2002). Promoting late-successional characteristics in harvested stands attempts to mimic influences of natural stand-replacing disturbances (storms, wildfires). Hence, GTR is a part of the strategy to achieve ecologically sustainable management by modifying forestry operations to accord better with natural-disturbance regimes (Lindenmayer and Franklin 2002).

An obvious aim of retaining trees is to provide habitat for wildlife. For example, although clear-cutting dramatically reduces the density and species richness of birds, the loss is smaller in sites where many trees have been left standing (e.g., Beese and Bryant 1999; Tittler et al. 2001), particularly for bole- and canopy-feeders (Johnson and Landers 1981). Retention trees also help to sustain communities of small mammals (Sullivan and Sullivan 2001) and macro-

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arthropods (Siira-Pietikäinen et al. 2003). When the trees die, they may host numerous saproxylic insects adapted to benefit from large-scale disturbances (Kaila et al. 1997; Siitonen et al. 2000).

In several Fennoscandian and North American studies it has been concluded that retention trees populated by epiphytic lichens and bryophytes may become centres of their recolonization in the next forest generation (Peck and McCune 1997; Hazell and Gustafsson 1999; Sillett and Goslin 1999; Keon and Muir 2002). This is especially important for those old-growth species whose populations are more limited by dispersal than by habitat availability or the ability to grow in young stands (Sillett et al. 2000; Hilmo and Såstad 2001; Rosso et al. 2001; Keon and Muir 2002). However, the dry, sunny, and windy conditions in clearcuts (Chen et al. 1999) may limit this "lifeboating" function, since lichens and bryophytes cannot regulate water loss (Green and Lange 1995) and incur a high risk of drying out. The risk is likely to depend on both epiphyte and tree species, given the strong phorophyte effects on epiphyte communities (e.g., Barkman 1958). For example, canopy-dwellers (such as alectorioid and usneoid lichens) may be well adapted to the open and sunny conditions found in clearcuts. In Sweden, transplants of two management-sensitive species — a bryophyte, *Antitrichia curtipendula* (Hedw.) Brid., and a lichen, *Lobaria pulmonaria* (L.) Hoffm., — survived on retained European aspen (*Populus tremula* L.) after 2 years (Hazell and Gustafsson 1999). In contrast, transplants of old-growth lichens *Lobaria oregana* (Tuck.) Müll. Arg. and *Pseudocyphellaria rainierensis* Imshaug on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) had a low growth rate and a high mortality rate in the GTR cuts in Oregon, USA (Sillett and McCune 1998). Clearly, additional comparative and quantitative studies are needed to assess the value of retention trees for epiphytes.

The aims of this study are (*i*) to compare the estimated short-term vitality of lichens and bryophytes on trees of different species in the middle and at the edge of GTR cuts and in adjacent forests, (*ii*) to assess the diversity of epiphytic species on retention trees, and (*iii*) to distinguish the epiphytic species that survive well on solitary retention trees. We explore bryophytes and lichens on four species of retention trees and adjacent forest trees in a hemiboreal area in Europe, and discuss the efficiency and limitations of retaining trees for cryptogam conservation.

Materials and methods

Study area

The study was carried out in four randomly selected state forest districts in central, eastern, and southern Estonia located at 58°–59°N and 25°–27°E (Fig. 1). Estonia is situated in the hemiboreal vegetation zone (Ahti et al. 1968); forests cover ca. 50% of the country and the terrain is flat. The mean air temperature is ca. 17 °C in July and –6.5 °C in January; the average precipitation is 600–700 mm per year. All studied districts comprise large but extensively managed forest areas below 75 m a.s.l. The dominating site types (sensu Paal 1997) are dry boreal (mainly *Vaccinium myrtillus* type) and mesoeutrophic (*Oxalis* and *Hepatica* types) in the central Estonian districts and eutrophic boreonemoral and

Fig. 1. Locations of the study areas in Estonia.

paludifying forests (mainly *Aegopodium* and *Filipendula* types) in the eastern districts.

Since 1999, the Estonian Forest Act has required the retention of at least 5 m³ of live and dead trees per clear-cut hectare. In state forests (38% of all forests), which are granted a certificate of sustainable forestry by the Forest Stewardship Council, this requirement has generally been fulfilled, though many of the live retention trees are young or vulnerable to windthrow. In the four districts we studied, 31% of live trees on GTR cuts (including seed trees) were birches (*Betula* spp.), 20% were Scots pine (*Pinus sylvestris* L.), 18% were European ash (*Fraxinus excelsior* L.), 14% were European aspen (hereinafter referred to as aspen), 7% were littleleaf linden (*Tilia cordata* P. Mill.), and 6% were other species (Rosenvald and Löhmus 2005). Most retained trees are solitary.

The study included all 103 stands that had been harvested during 2001–2002 in the four forest districts. In spring 2002, all live trees and snags with a diameter at breast height (DBH) >13 cm were mapped, their species, DBH, age, and condition were recorded, and the type, size, and age of the cuts were determined. The mean area of the cuts was 2.3 ha (range 0.2–6.6 ha) and there were, on average, 20 (2–57) live trees·ha⁻¹. The age range of retention trees was mostly between 50 and 80 (maximum 110) years for deciduous trees and between 90 and 110 (maximum 180) years for pines. Most of the harvested stands had been of eutrophic boreonemoral (*n* = 47), dry boreal (*n* = 22), or mesoeutrophic type (*n* = 10).

Study design and sampling

Sampling included two steps: (1) random sampling of the four most common retention-tree species to record changes in the total cover and vitality of lichens and bryophytes between two years; and (2) random sampling of two deciduous tree species (aspen and birch) with contrasting patterns of

cryptogam vitality to explore the species composition in detail.

There were 32 harvested stands where ashes had been retained; 30 GTR cuts were preselected also for the more numerous tree species. Depending on which tree species co-occurred, by chance, in the same GTR cuts (we then sampled all species on the same cuts), the true sample sizes differed slightly between the species. Thus, 33 GTR cuts were sampled for Scots pine, 31 were sampled for birches and aspen, and 29 remained for ash (3 had no trees either in the middle or at the edge of the cut). In each GTR cut, three live trees of the same species and similar in size (DBH) were selected at random, one each from (*i*) the middle of the cut (>25 m from the forest edge), (*ii*) the periphery of the cut (5.5 ± 2.8 m (mean ± SD) from the forest edge), and (*iii*) the adjacent forest of the same type (>25 m from the cut edge). The use of distances >25 m is likely to eliminate the steepest microclimatic gradients of the forest edge (e.g., Gignac and Dale 2005); longer distances would have often produced marked differences in stand conditions or tree characteristics. Four of the trees fell during the study and the total sample included 368 trees in or around 85 GTR cuts. The average DBH of the sample trees was 33 cm (range 14–90 cm).

In step 2 we studied the composition of cryptogam species only on aspen and birch because they appeared to differ in several important patterns (cover of bryophytes, vitality of lichens; see Results). For both tree species, we explored 31 retention trees (mostly in the middle of the GTR cuts) and 31 adjacent forest trees (the same trees as in step 1). The two tree species co-occurred in 13 GTR cuts.

Field and laboratory work

For step 1, the cover (%) and vitality of lichens and bryophytes were estimated visually by the second author in four 20 cm × 20 cm plots on each tree, centred on heights of 0.2 and 1.3 m on the northern and southern sides of the trunk. The plots were surveyed twice (early summer in 2003 and 2004); their exact location on trees was marked for reanalysis. To quantify vitality, the proportion of the total cover that was desiccated was estimated according to the colour (bleaching) and structure (e.g., broken or dead parts) of shoots or thalli (in microlichens, including apothecia).

For step 2, in summer 2004 (second or third postharvest year), cryptogam species were recorded by the first author on the trunks of aspens and birches. Because the individual species (particularly those of conservation concern) cover only minor and often imprecisely delineated parts of the trunk, the presence and condition of each species were visually assessed on the whole trunk between heights of 0.2 and 1.8 m. Damage was ranked according to Hedenås and Ericson (2003; slightly modified): 0, no deviation from normal colour and thus no desiccation damage; 1, few visible colour changes; 2, large patches with colour changes; 3, severe bleaching or thalli and shoots either dead or lost. Species whose average damage scores were >1 are "sensitive" for the purposes of this study; this term does not necessarily mean that they are threatened by forestry.

Nomenclature follows Ingerpuu and Vellak (1998) for bryophytes and Randlane et al. (2004) for lichens. Lichenicolous *Bispora* species were considered lichens, *Lepraria* and *Ulota*

species were treated collectively, and one specimen of *Mycomicrothelia* was identified only to the genus. We distinguished key habitat indicator species (sensu Nitare 2000) and species that are rare in Estonia (sensu Ingerpuu and Vellak 1998; Randlane and Saag 1999; Jüriado et al. 2000) as species of conservation concern.

Data analyses

The cover of both bryophytes and lichens was strongly positively correlated between the northern and southern sides of the trunk as well as between the two heights (Spearman's correlation coefficients, $r_S = 0.41$–0.73, $n = 368$, $P < 0.001$). At both heights and for both taxa, cover was greater on the northern than on the southern side (Wilcoxon's matched-pairs tests, $P < 0.001$). On both sides, bryophytes were more abundant at 0.2 m height than at breast height (Wilcoxon's test, $P < 0.001$); there was no such clear difference for lichens. Given the general aims of our study and the similar vitality of cyanolichens on the two sides of retention trees (Blomberg 2002), we pooled these interdependent estimates from the different plots on each trunk into one average value. We admit, however, that aspect may influence the vitality of more sensitive taxa (e.g., Hazell and Gustafsson 1999) and deserves special attention after these taxa have been distinguished.

Next, we calculated the exponential rate of change in the vitality of thalli (shoots), v, within 2 years on each tree: $v = \ln(A_2(1 - p_d)/A_1)$, where A_1 and A_2 are the total coverage (proportion) of all species of lichens or bryophytes 1 and 2 years after harvesting, respectively, and p_d is the proportion of the total cover that was damaged in the second year; v is analogous to the exponential rate of population increase that is widely used in population ecology (e.g., Caughley and Sinclair 1994). The formula takes into account our inability to measure the cover prior to logging — we related the final cover of healthy thalli and shoots ($A_2(1 - p_d)$) to the total cover in the first year (A_1) because some dead parts of thalli or shoots were likely to be broken and lost by the second year. However, we assumed that these parts were present (though desiccated) 1 year after harvesting. To see whether (and to what extent) desiccation occurred in the forest before clear-cutting, we included the adjacent forest trees in the analysis as a reference group. Note that v cannot be divided into annual amounts because we have no actual measurements of the changes during the first postlogging year.

To examine the extent of damage, we omitted trees with very few epiphytes and species with very low occurrence, to reduce noise. (*i*) For analyzing v with respect to tree location and tree species, we considered only the trees where the initial cover (A_1) of bryophytes and (or) lichens exceeded 10%. The drawback of this procedure was the large number of missing values; for example, only one Scots pine had such a high cover of bryophytes, and we had to omit all pines from bryophyte analyses. (*ii*) To compare the vitality of different cryptogam species, we considered the average damage scores (0–3) of each of the 24 lichen and 19 bryophyte species that occurred at least three times on both forest and retention trees. Note that we use the latter mean values only for comparing species or sites; these should not be interpreted at an absolute scale, since the intervals between the damage classes are not equal.

We used parametric statistical methods for hypothesis testing; the assumptions of normal distribution (Kolmogorov–Smirnov test) and the homogeneity of variances (Levene's test) were checked prior to analysis. The tests were performed with Statistica® 6.0 software (StatSoft, 1984–2001). All confidence intervals (CI) given are at 95% probability.

The effect of tree species on the total cover of lichens or bryophytes on forest trees (the assumed preharvest situation) was explored using one-way ANOVA. The cover values (proportions) were arcsine square root transformed, but we present descriptive statistics in their untransformed state for ease of interpretation. Two-way ANOVA was used to assess the effects of tree species and location relative to harvested area on v. Although the distributions of v deviated from normal (Kolmogorov–Smirnov test, $P < 0.01$) with positive kurtosis (2.6 ± 0.4 (mean $\pm$ SE) for bryophytes and 3.9 ± 0.3 for lichens), we used ANOVA for its better illustrative opportunities and the possibility of testing for interactions. The F statistic is fairly robust to assumptions of normality and positive kurtosis leads to smaller, not larger, F values (and consequently, a more conservative test; Lindman 1974). In this case, we also analyzed the main effects with Kruskal–Wallis ANOVAs, which gave similar results to the parametric tests. In ANOVA, post hoc comparisons were made using Tukey's honestly significant difference tests. To compare v values between lichens and bryophytes on the same trees, we used the t test for paired samples.

General linear models were used to detect the extinction of cryptogams on 31 retained aspens and 31 birches, based on pairwise comparisons with adjacent forest trees. The dependent variable was the relative species richness of bryophyte or lichen species on retention trees (the number of species on each retention tree minus the number of species on the forest tree adjacent to it); tree species and relative diameter (DBH of the retention tree minus DBH of the adjacent forest tree) were included as independent factors. We rejected the null hypothesis of no loss if, after these confounding factors were taken into account, the intercept of the model deviated significantly from zero.

Results

General decline of cryptogam vitality on retention trees

The change in vitality (v) of lichens on 325 trees depended on the location of the latter relative to the GTR cut ($F_{[2,313]} = 7.8$, $P < 0.001$) and on the tree species ($F_{[3,313]} = 3.8$, $P = 0.010$). In general, their vitality decreased along the forest – GTR cut gradient; however, the difference between the edge of the harvested area ($v = -0.03 \pm 0.05$ (CI)) and either extreme (forest: $v = 0.04 \pm 0.05$; centre of the GTR cut: $v = -0.10 \pm 0.05$ (CI)) was not significant (Tukey's test, $P = 0.11$–0.13). The interaction between location and tree species was also clear ($F_{[6,313]} = 2.6$, $P = 0.018$): the change occurred only on birch and pine (Fig. 2A), with the greatest decline on birch and no decline on aspen (Tukey's test for these extremes in the middle of the cut, $P = 0.047$).

The change in vitality of bryophytes on 182 deciduous trees was highly affected by tree location ($F_{[2,173]} = 14.7$, $P < 0.001$): the value at the centre of the GTR cut ($v = -1.24 \pm 0.47$; CI) did not differ from that at the edge ($v = -1.12 \pm 0.60$; CI; Tukey's test, $P = 0.44$), but in both of

Fig. 2. Mean exponential rate of change in vitality (v; 95% CI) of lichens (A) and bryophytes (B) according to tree species and location (forest or green tree retention (GTR) sites). The numbers above the bars are sample sizes. Note that bryophytes were not studied on Scots pine and that the graphs have different scales.
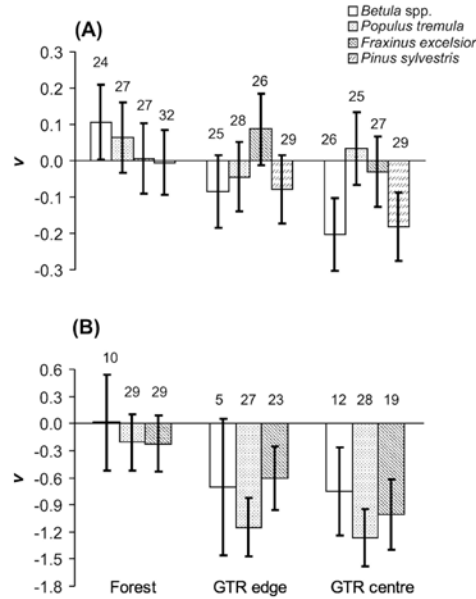
these locations the bryophytes were far less healthy than in forest ($v = -0.37 \pm 0.46$ (CI); $P < 0.001$). The interaction between location and tree species was not significant ($F_{[4,173]} = 0.8$, $P = 0.53$), and the main effect of tree species was only marginal ($F_{[2,173]} = 2.8$; $P = 0.064$) — bryophytes tended to be more suppressed on aspen than on ash (Tukey's test, $P = 0.069$) and birch ($P = 0.088$; Fig. 2B).

On 102 retention trees, the initial cover of both bryophytes and lichens exceeded 10%. The average exponential decline in the vitality of bryophytes ($v = -0.94 \pm 0.21$ (CI)) was dramatically greater there than the decline in the vitality of lichens ($v = -0.02 \pm 0.06$; paired t test, $t_{[101]} = 8.2$, $P < 0.001$). Hence, the relative decrease in healthy cover within 2 years ($1 - e^v$) was, on average, 2% for lichens but 60% for bryophytes — a 30-fold difference.

There was no significant reduction in the vitality of cryptogams on forest trees of any species (Fig. 2); lichen thalli even tended to grow on birches during the 2 years ($v = 0.11 \pm 0.10$ (CI)). The mean cover of epiphytes on forest trees (Fig. 3) differed widely between the tree species ($F_{[3,238]} = 18.1$, $P < 0.001$) and between lichens and bryophytes (main effect: $F_{[1,328]} = 80.2$, $P < 0.001$; interaction with tree species: $F_{[3,328]} = 56.9$, $P < 0.001$). The cover

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Table 1. General linear models explaining the difference in epiphytic species richness per trunk between retention trees and forest trees.

Independent variable	Bryophytes ($n = 62$)			Lichens ($n = 62$)		
	Coefficient (mean ± SE)	$F_{[1,58]}$	P	Coefficient (mean ± SE)	$F_{[1,58]}$	P
Intercept	−1.42±0.36	15.1	<0.001	−0.24±0.52	0.2	0.640
Tree species[a]	−0.65±0.36	3.2	0.078	−1.00±0.52	3.7	0.059
Difference in diameter	0.04±0.03	1.4	0.245	−0.02±0.05	0.2	0.668
Tree species × difference in diameter	0.04±0.03	1.6	0.206	0.11±0.05	5.1	0.027

Note: Each observation consists of one retention tree and one tree of the same species and approximately the same size in adjacent forest. Species and differences in diameter (between retention tree and forest tree) are included as covariables; the intercept indicates the adjusted difference between retention trees and forest trees.

[a]Aspen (1) compared with birch (0).

Fig. 3. Mean cover (95% CI) of lichens and bryophytes on forest trees of different species. The sample included 31 birches, 33 Scots pine, 31 European aspen, and 29 European ash.

Fig. 4. Linear regressions between the average damage scores of the 19 bryophyte (○, broken line) and 24 lichen species (●, solid line) that had at least three occurrences on forest and retention trees in both locations ($P_{intercept} = 0.11$, $P_{slope} < 0.001$, $R^2 = 0.53$ for lichens and $P_{intercept} < 0.001$, $P_{slope} = 0.27$, $R^2 = 0.07$ for bryophytes). Numbers beside the data points indicate the number of species with similar values.

of lichens did not differ between the deciduous tree species, but lichens occupied significantly larger areas on pines than on aspens (Tukey's test, $P < 0.001$) and birches ($P = 0.016$). In contrast, pines had almost no bryophytes and birches had few, while aspens and ash were similarly well covered with bryophytes (Fig. 3).

Species composition and species-specific vitality on aspens and birches

Altogether, 45 bryophyte and 74 lichen species or species-groups (including one lichenicolous fungus) were recorded on the 62 aspens and 62 birches in 31 forests and 31 GTR cuts (see the Appendix). The total species richness of cryptogams was similar on forest trees and retention trees (95 and 94 species, respectively). However, retention trees had fewer bryophyte species per trunk (3.6 ± 0.6 (CI)) than forest trees (4.7 ± 0.7 (CI)); however, no difference was found for lichens (5.7 ± 0.7 and 5.6 ± 0.7 (CI), respectively). Linear models, which took into account the tree species and differences between the DBHs of retention trees and forest trees, indicated that species loss had been highly significant for bryophytes (1.4 ± 0.7 (CI) species per trunk) but not for lichens (0.2 ± 1.1 (CI) species per trunk) on the retention trees within 2 years (Table 1).

Aspens were clearly more species-rich (73 species in forest, 72 in GTR cuts) than birches (47 and 41 species, respectively). Altogether, 63 of 94 species occurred only on aspens, including 9 rare or indicator taxa: the bryophytes *Frullania dilatata* (L.) Dum., *Neckera pennata* Hedw., and the lichens *Acrocordia cavata* (Ach.) R.C. Harris, *Acrocordia gemmata* (Ach.) A. Massal., *Leptogium saturninum* (Dickson) Nyl., *Leptogium teretiusculum* (Wallr.) Arnold, *Megalaria grossa* (Pers. ex Nyl.) Hafellner, and *Opegrapha rufescens* Pers. Out of 56 species on birches, 25 were unique, only 2 of these with indicator value (the lichens *Arthonia leucopellaea* (Ach.) Almq. and *Mycoblastus sanguinarius* (L.) Norman).

The causes of damage appeared to differ between lichens and bryophytes, given the contrasting relationships between the average damage scores of the same species on retention trees and forest trees (Fig. 4). For lichens, the damage in harvested stands hardly differed from that in forests (intercept of the regression line, $P = 0.11$); instead, 53% of variation was explained by the general sensitivity of the same species — the damage varied proportionately in both sites (slope: 1.03 ± 0.20 (mean ± SE), $P < 0.001$). For bryophytes, the trend of general sensitivity of species was

nonsignificant and nonproportional (slope: 0.47 ± 0.41(mean ± SE), P = 0.27), and the damage was significantly greater in GTR cuts than in forests, particularly for the species that were relatively healthy in forests (intercept: 1.17 ± 0.21(mean ± SE), P < 0.001; Fig. 4).

Crustose lichens (e.g., *Buellia griseovirens* (Turner & Borrer ex Sm.) Almb., *Loxospora elatina* (Ach.) A. Massal., *Megalaria grossa*, and *Ropalospora viridis* (Tønsberg) Tønsberg), and some macrolichens with small foliose (*Vulpicida pinastri* (Scop.) J.-E. Mattsson & M.J. Lai) or podethial thalli (*Cladonia coniocraea* (Flörke) Spreng.), were healthy everywhere. On the other hand, the mean damage score for 13 species was >1.0 in both the forest and the GTR cuts (Fig. 4; for the species list see the Appendix). The 10 sensitive bryophyte species were mainly mosses and hepatics that form distinct mats and wefts (e.g., *Homalia trichomanoides* (Hedw.) Schimp. in B.S.G., *N. pennata*, *Pylaisia polyantha* (Hedw.) Grout, and *Radula complanata* (L.) Dumort.). The three sensitive lichen species (*Lecanora allophana* Nyl., *Parmelia sulcata* Taylor, and *Peltigera praetextata* (Flörke ex Sommerf.) Zopf) were unhealthy in both the forest and the GTR cuts, probably because of factors other than logging.

Discussion

Although species richness on GTR cuts did not differ from that in forests at the landscape scale, we found that some cryptogams suffered mortality on retention trees, with local extinctions within 2 years of harvest. In the absence of preharvest data for comparison, and given no evidence of a net decline in vitality in adjacent forest trees over 2 years, total epiphyte cover in the forest 1 year after logging was deemed to be an acceptable reference value. We are therefore confident that the average changes in epiphyte vitality that we report can be attributed to logging.

We documented wide variation in responses to GTR cutting between and among lichen and bryophyte species at the centre and edge of the cuts and on different tree species. The negative impacts were severe and almost independent of tree species for bryophytes throughout the GTR cuts, but were weaker for lichens, particularly at the edges of the cuts and on aspen and ash. Such interactions may partly explain the controversial views about logging impacts on cryptogams. For example, several studies have reported decreased abundance, cover, growth, vitality, or biomass of epiphytic cryptogams, even after partial cutting (e.g., Thomas et al. 2001; Coxson et al. 2003; Hedenäs and Ericson 2003) or near clearcuts (Hilmo and Holien 2002; Rheault et al. 2003). Yet some transplantation experiments have demonstrated their high survival rates on retention trees in GTR cuts or in young forests (Hazell and Gustafsson 1999; Gauslaa et al. 2001; Hilmo 2002).

The negative effects of clear-cutting on epiphytic lichens have been documented in several studies (Esseen et al. 1997; Berglund and Jonsson 2005), but our data showed that the decrease of their total cover on retention trees is relatively small. The lower confidence limits of *v* indicated 8% maximum loss for lichens compared with 68% for bryophytes. The resistance of lichens to desiccation could be explained by their ability (*i*) to attain positive net photosynthesis using only air humidity, while bryophytes need liquid water (Green and Lange 1995), and (*ii*) to recover from and adjust to bright light by increasing thallus thickness and (or) the concentration of pigments, which act as a sunscreen for photobiont cells against excessive UV radiation (Rikkinen 1995; Gauslaa and Solhaug 2001; Hilmo 2002). Hence, many forest lichens obviously can survive on GTR cuts if suitable substrata are available; the crucial question is, which species can and which cannot? The resistant species are likely to include cyanolichens, whose biomass is higher in regenerated stands with retained trees than in those without (Peck and McCune 1997), the light-tolerant Parmeliaceae, and canopy-dwelling alectorioid species; and possibly also usneioid species that experience a moderate level of photoinhibition with high light intensity (Gauslaa and Solhaug 1996). Green-algal lichens are probably much more stressed in open environments, though they can probably survive under some conditions (e.g., *Sphaerophorus globosus* (Hudson) Vainio is most abundant near old remnant trees in forests; Sillett and Goslin 1999). In our analysis, the few sensitive lichen species did not belong to distinct morphological or habitat types. Moreover, these species tended to be equally damaged both in the forest and on retention trees, i.e., they were affected mostly by processes other than logging. For example, apothecia of *Lecanora allophana* were frequently bleached or broken, apparently eaten by snails (personal observation; cf. Baur et al. 1994).

In contrast to lichens, epiphytic bryophytes were very sensitive to sudden changes in humidity and light conditions on retention trees. A similar rapid loss of ground mosses in clearcuts has been previously reported (Jalonen and Vanha-Majamaa 2001). Generally, bryophytes' requirements for light and water are closely determined by their life-form (Mägdefrau 1982): cushions predominate in open sites (such as on free-standing trees), whereas mats, wefts, and fans are shade-lovers (e.g., on tree bases). Indeed, the mat- and weft-forming mosses and hepatics (e.g., *Brachythecium velutinum* (Hedw.) Schimp. in B.S.G., *Homalia trichomanoides*, *Radula complanata*) were the most sensitive in our study — they were healthy in forests and heavily damaged on retention trees. Also Hazell and co-authors (1998) have pointed out the low tolerance of the weft-forming *Pylaisia polyantha* and *Radula complanata* to low humidity compared with the cushion-forming *Orthotrichum speciosum* Nees in Sturm and *Nyholmiella obtusifolia* Brid.

Although the structure of epiphyte communities is strongly influenced by the texture, chemistry, and moisture content of the bark of host tree species (e.g., Barkman 1958), the condition of epiphytes on retention trees of different species has not been compared before. We found generally healthier lichens on retained aspens and ash than on birch and pine. Probably the relatively coarse bark of aspens and ash provides better shade, but aspens also have a distinct epiphyte species composition (e.g., Kuusinen 1996). For bryophytes, unsuitable moisture conditions at a larger (stand) scale could prevail over the microclimatic or bark characteristics of a particular host species (e.g., Potzger 1939; Frisvoll and Presto 1997; Thomas et al. 2001). For example, the relative abundance of bryophytes on conifers has been found to be limited more by moisture content at the stand scale than by bark pH (Hong and Glime 1997).

Practical implications and conclusions

No study has covered the mortality of epiphytes on retained trees within the 10–20 years following GTR cutting until the new stand starts providing shade. Hence, there is no conclusive answer to whether lichens really survive and whether bryophytes can adapt to postharvest conditions and ultimately recover. The current success stories concern the examination of cryptogam transplants on retention trees only 1–2 years postharvest, which may be too short a time to detect their slow death via sustained photoinhibition or acclimation and recovery (see Hazell and Gustafsson 1999; Gauslaa et al. 2001). However, drastic short-term differences in condition among different taxa, such as those documented by us, are likely to provide them with rather different prospects for the future. Hence, our results strongly suggest that GTR can be a successful conservation tool for lichens, particularly many microlichens on aspens and ash. Although Tønsberg (1992) considered the taxa with sorediate or granulous thalli to be prone to desiccation, this may perhaps pose a problem only for the inhabitants of humid tree bases, such as *Mycobilimbia* (Hedenäs and Ericson 2003). The sorediate species growing higher on the trunk (e.g., *Biatora efflorescens* (Hedl.) Räsänen, *Loxospora elatina*, *Ropalospora viridis*) were robust in our study, as were several microlichens of conservation concern (*Acrocordia cavata*, *Acrocordia gemmata*, *Megalaria grossa*, *Mycoblastus sanguinarius*).

In principle, the omission of trees with less than 10% lichen cover from samples may have led to overly optimistic results, because the issue is controversial. Gauslaa and Solhaug (1998) showed that larger thalli of the folious cyanobacterial lichen *Degelia plumbea* (Lightf.) P. M. Jørg. & P. James had higher water-holding capacity than smaller thalli. In contrast, young thalli of *Lobaria pulmonaria* were larger on clearcuts (4 years after logging) than in young or old-growth stands (Sillett et al. 2000). Hence, foliose lichens may have survived less well on the sparsely inhabited trees (which we did not sample); however, we did not observe this at the species level (species with small foliose or podethial thalli, such as *Vulpicida pinastri* and *Cladonia coniocraea*, were healthy on retained trees). Thus, it could be important to retain, in particular, those trees that already have a well-developed cover of lichens. This often coincides with the retention of old trees, which can also host desiccation-prone and threatened epiphytes (e.g., *Leptogium teretiusculum* and *Ulota* spp.; see also McGee and Kimmerer 2002), and may intercept spores or other propagules more effectively (Hazell et al. 1998).

Tree species and their epiphyte communities vary geographically and exact recommendations for GTR should be assessed at a regional scale. Among the retained species studied by us in Estonia, aspens and ash produced the best results: they had a relatively high cover of cryptogams, and lichens certainly survived best on these tree species. We recorded several unique and rare species on aspen, supporting reports of diverse and unique communities on this species in boreal forests (e.g., Kuusinen 1996; Hedenäs 2002; Jüriado et al. 2003). On the other hand, since ash survives better than aspen on the GTR cuts (Rosenvald and Löhmus 2005) and its lichen flora resembles that of aspen (Löhmus 2003), ash may provide a more reliable "lifeboat" in the long term.

It will be important to study what proportion of threatened forest lichens could be protected using these two tree species.

Retention of single trees does not appear to provide sufficient protection for bryophytes, at least in the short term; notably, weft-, fan-, and mat-forming species have a high risk of dessication. Retaining trees near edges (this study) or in groups (Hazell and Gustafsson 1999) or using shelterwood cutting (Hannerz and Hånell 1997) may increase the value of retained trees in conservation of epiphytes, but further research is needed. Retention of groups of trees also has operational advantages over single-tree retention (Hazell and Gustafsson 1999), so the principal question concerns the size of group required to moderate microhabitat (Fenton and Frego 2004), resist windfall (Esseen 1994), and meet the requirements of other taxa (Beese and Bryant 1999). In Estonia, for example, the current GTR cuts are too small (2.3 ha, on average, in our study districts) for large patches to be retained within them. Research is required to determine whether such a fine-grained landscape mosaic may eventually lead to the extinction of forest-interior species, including bryophytes.

Acknowledgements

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Appendix A

Appendix appears on following page.

Table A1. Numbers of occurrences of bryophyte and lichen species (healthy (V) or at least partly damaged (D)) on aspens and birches in forest and green-tree-retention (GTR) cuts, and percentages of records with signs of damage ($\Sigma D/\Sigma(D + V)$).

| | Forest | | | | GTR cut | | | | |
| | Aspen ($n = 31$) | | Birch ($n = 31$) | | Aspen ($n = 31$) | | Birch ($n = 31$) | | Total damage (%) |
	V	D	V	D	V	D	V	D	
Bryophytes									
Amblystegium serpens	3	0	—	—	0	2	—	—	40
Amblystegium subtile*	5	3	1	1	1	6	—	—	59
Brachythecium populeum	—	—	—	—	1	0	—	—	0
Brachythecium reflexum	1	0	—	—	—	—	—	—	0
Brachythecium rutabulum†	4	0	—	—	1	1	0	1	29
Brachythecium salebrosum	1	0	—	—	2	2	—	—	40
Brachythecium velutinum*	3	0	—	—	1	5	—	—	56
Calypogeia integristipula	—	—	—	—	—	—	0	1	100
Campylium sommerfeltii	1	0	—	—	2	1	—	—	25
Cirriphyllum piliferum	4	0	—	—	2	0	—	—	0
Climacium dendroides	4	0	—	—	0	1	—	—	20
Dicranum montanum†	7	0	15	0	3	0	11	8	18
Dicranum scoparium†	5	0	20	0	1	0	4	11	27
Eurhynchium angustirete†	2	1	—	—	2	1	—	—	33
Eurhynchium hians†	6	2	1	0	4	3	—	—	31
Eurhynchium pulchellum	2	0	—	—	0	1	—	—	33
Fissidens adianthoides	3	0	—	—	2	0	—	—	0
Frullania dilatata	—	—	—	—	1	0	—	—	0
Herzogiella seligeri	—	—	—	—	—	—	1	0	0
Homalia trichomanoides*	4	0	—	—	0	7	—	—	64
Hylocomium splendens†	3	2	—	—	1	3	—	—	56
Hypnum cupressiforme*	8	7	4	2	2	8	1	1	55
Hypnum pallescens	1	0	—	—	—	—	—	—	0
Jamesoniella autumnalis	—	—	1	0	—	—	—	—	0
Lepidozia reptans	—	—	2	1	—	—	—	—	33
Lophocolea heterophylla	1	0	4	1	—	—	0	1	29
Neckera pennata*	6	1	—	—	1	8	—	—	56
Orthotrichum gymnostomum	—	—	—	—	1	0	—	—	0
Orthotrichum speciosum*	14	2	—	—	5	9	—	—	37
Plagiomnium cuspidatum*	4	3	1	1	4	2	1	1	41
Plagiothecium curvifolium	—	—	0	1	—	—	—	—	100
Plagiothecium laetum	—	—	3	1	—	—	1	0	20
Pleurozium schreberi*	—	—	5	0	—	—	2	6	46
Pseudoleskeella nervosa	—	—	—	—	0	1	—	—	100
Pilidium pulcherrimum†	2	3	13	7	—	—	8	7	43
Pilium crista-castrensis	1	0	—	—	—	—	—	—	0
Pylaisia polyantha*	11	7	2	1	4	12	0	2	56
Radula complanata*	10	15	1	0	0	24	0	1	78
Rhodobryum roseum	3	1	—	—	—	—	—	—	25
Rhytidiadelphus triquetrus†	7	2	0	1	1	3	—	—	43
Sanionia uncinata†	12	2	1	0	3	4	1	0	26
Tetraphis pellucida	—	—	1	0	—	—	—	—	0
Thuidium delicatulum	2	0	—	—	—	—	—	—	0
Thuidium philibertii	3	1	—	—	0	2	—	—	50
Ulota spp.	—	—	—	—	1	0	—	—	0
Lichens									
Acrocordia cavata	2	0	—	—	1	0	—	—	0
Acrocordia gemmata	—	—	—	—	2	0	—	—	0
Anaptychia ciliaris	0	3	—	—	1	0	—	—	75
Arthonia leucopellaea	—	—	—	—	—	—	1	0	0
Arthonia spadicea	1	0							0

Table A1 (continued).

| | Forest | | | | GTR cut | | | | |
| | Aspen ($n = 31$) | | Birch ($n = 31$) | | Aspen ($n = 31$) | | Birch ($n = 31$) | | Total damage (%) |
	V	D	V	D	V	D	V	D	
Arthopyrenia punctiformis	—	—	—	—	1	0	—	—	0
Arthothelium ruanum	1	0	—	—	—	—	—	—	0
Bacidia arceutina	3	0	—	—	2	0	—	—	0
Bacidia fraxinea	—	—	—	—	1	0	—	—	0
Bacidia rubella	1	0	—	—	—	—	—	—	0
Bacidia subincompta	—	—	—	—	4	0	—	—	0
Biatora efflorescens†	1	0	3	0	—	—	4	0	0
Bispora sp.	—	—	—	—	1	0	—	—	0
Buellia griseovirens†	3	0	14	0	1	0	11	0	0
Caloplaca cerina	—	—	—	—	1	0	—	—	0
Caloplaca flavo-rubescens†	7	1	—	—	10	2	—	—	15
Chaenotheca trichialis	—	—	1	0	—	—	—	—	0
Cladonia cenotea	—	—	3	0	—	—	5	1	11
Cladonia chlorophaea	1	0	1	0	—	—	—	—	0
Cladonia coniocraea†	7	0	22	2	3	0	16	11	21
Cladonia digitata†	—	—	4	0	—	—	7	7	39
Cladonia fimbriata†	6	0	6	0	4	0	5	0	0
Cladonia ochrochlora	—	—	—	—	—	—	1	0	0
Cladonia sp. (prothalli only)	1	0	1	0	—	—	1	0	0
Dimerella pineti	1	0	2	0	—	—	—	—	0
Graphis scripta	—	—	1	0	1	1	2	0	20
Hypogymnia physodes†	—	—	16	7	0	2	7	16	52
Imshaugia aleurites	—	—	1	0	—	—	—	—	0
Lecania cyrtella	—	—	—	—	1	0	—	—	0
Lecanora allophana*	3	6	—	—	5	7	—	—	62
Lecanora argentata	2	2	1	0	0	1	0	1	57
Lecanora expallens	1	0	—	—	1	0	1	0	0
Lecanora pulicaris†	—	—	6	0	—	—	6	0	0
Lecanora rugosella†	4	0	—	—	2	1	—	—	14
Lecidea nylanderi†	—	—	22	0	—	—	24	1	2
Lecidella elaeochroma	2	0	—	—	1	0	—	—	0
Lecidella euphorea	6	1	—	—	2	0	—	—	11
Lepraria spp.†	16	1	19	0	5	8	14	1	16
Leptogium saturninum	0	1	—	—	1	0	—	—	50
Leptogium teretiusculum	—	—	—	—	1	0	—	—	0
Loxospora elatina†	—	—	11	0	—	—	11	1	4
Megalaria grossa†	4	0	—	—	4	0	—	—	0
Melanelia exasperatula	0	1	—	—	2	0	—	—	33
Melanelia subaurifera	—	—	—	—	0	1	—	—	100
Micarea prasina	2	0	4	0	—	—	—	—	0
Mycobilimbia carneoalbida	3	0	—	—	—	—	—	—	0
Mycobilimbia epixanthoides	2	0	—	—	2	0	—	—	0
Mycobilimbia sabuletorum	1	0	—	—	—	—	—	—	0
Mycobilimbia tetramera	—	—	—	—	1	0	—	—	0
Mycoblastus fucatus†	—	—	3	0	1	0	5	0	0
Mycoblastus sanguinarius	—	—	1	0	—	—	1	0	0
Mycomicrothelia wallrothii	—	—	—	—	—	—	1	0	0
Mycomicrothelia sp.	—	—	—	—	2	0	—	—	0
Ochrolechia microstictoides	—	—	1	0	—	—	—	—	0
Opegrapha rufescens	1	0	—	—	1	1	—	—	33
Parmelia saxatilis	—	—	—	—	—	—	1	0	0
Parmelia sulcata*	—	—	1	5	0	2	0	1	89
Parmeliopsis ambigua†	—	—	5	0	—	—	13	0	0

Table A1 (*concluded*).

| | Forest | | | | GTR cut | | | | |
| | Aspen (*n* = 31) | | Birch (*n* = 31) | | Aspen (*n* = 31) | | Birch (*n* = 31) | | Total damage (%) |
	V	D	V	D	V	D	V	D	
Peltigera canina	0	1	—	—	—	—	—	—	100
Peltigera membranacea	1	0	—	—	—	—	—	—	0
*Peltigera praetextata**	2	3	—	—	1	4	—	—	70
Pertusaria amara[†]	3	0	2	1	5	0	—	—	9
Pertusaria coccodes	—	—	—	—	1	0	—	—	0
Pertusaria leioplaca	0	1	—	—	—	—	—	—	100
Phlyctis argena[†]	27	0	4	0	23	0	—	—	0
Physcia stellaris	1	0	—	—	—	—	—	—	0
Physcia tenella	1	1	—	—	1	0	—	—	33
Physconia distorta	0	6	—	—	—	—	—	—	100
Platismatia glauca	—	—	1	1	—	—	0	2	75
Ramalina farinacea[†]	2	1	—	—	8	0	—	—	9
Ropalospora viridis[†]	3	0	15	0	1	0	10	0	0
Usnea hirta	—	—	—	—	—	—	1	0	0
Vulpicida pinastri[†]	—	—	11	0	—	—	16	0	0
Xanthoria parietina	0	1	0	0	2	0	—	—	33

Note: The 43 species that occurred on at least three forest and three retention trees are classified as either sensitive (*; average damage score >1 in either forest or GTR cut) or tolerant ([†]; other species; see Fig. 4).

Breeding birds in hemiboreal clear-cuts: tree-retention effects in relation to site type

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Summary

The variability of natural disturbance regimes implies that retention cutting, aimed at emulating natural disturbances to support biodiversity, should be forest-type specific. We explored in four site types (ranging from dry nutrient-poor to wet nutrient-rich) in Estonia how the retention of live and dead trees affects post-cut abundance and species richness of birds. The whole bird communities and harvest-sensitive species groups responded differently: while the total abundance and relative species richness of birds increased along with the abundance of dead trees, the species of national conservation concern occurred more frequently at higher densities of live trees. Hence, although the species of conservation concern and hole-nesters preferred the cuts having the generally densest and most species-rich avian communities, this co-variation was obviously insufficient for using the total community characteristics (particularly density) as indicators of forestry impacts on bird biodiversity. In contrast to expectations, tree retention always influenced birds independently of forest type. This may be related to the particular study system (notably low retention levels) but future studies should nevertheless explicitly address to what extent forest species are adapted to natural disturbances, and in which cases that knowledge can be used for forestry planning.

Introduction

Intensive management of boreal and temperate forests changes their structure and bird communities at several scales, including the reduction of viability or even regional extinction of the most demanding species (Imbeau *et al.*, 2001; Virkkala, 2004). To reduce the losses of biodiversity, silviculture should be modified towards greater resemblance to natural disturbance regimes (Lindenmayer and Franklin, 2002), such as variable retention cutting (VRC), which is an alternative to conventional clear-cutting. VRC attempts to emulate natural stand-replacing disturbances by preserving structural features of old forests – live and dead trees of varying sizes, multiple canopy layers and coarse woody debris (Franklin *et al.*, 1997).

Natural disturbance regimes vary across geographical regions (Bergeron *et al.*, 2002; Lorimer and White, 2003) and between forest types (Angelstam, 1998; Lõhmus *et al.*, 2004; Wallenius *et al.*, 2004), which implies corresponding differences in the adaptations of biota (Denslow, 1980;

Schmiegelow *et al.*, 1997) and, consequently, a necessity to use type-specific and locally adapted silvicultural techniques (Fries *et al.*, 1997; Angelstam, 1998). Yet, the impacts of clear-cutting and VRC on biodiversity have not been compared in sites having different natural disturbance regimes, though at least 48 recent studies report the general tree-retention effects on birds alone (Rosenvald and Lõhmus, 2007). The lack of such field tests is particularly remarkable given that the distinctness of avian communities of different forest types is well known (Haapanen, 1965; Petty and Avery, 1990) and their response to cutting is often found to depend on the tree-species composition of stands (Harrison *et al.*, 2005; Schieck and Song, 2006). Additionally, though the total density and species richness may indicate some changes in bird communities, the fate of particular species groups has more relevance for biodiversity conservation – yet, it has been seldom explored. For example, tree retention often supports hole-nesting birds (Carlson, 1994), but not necessarily all species. Moreover, with the exception of three Scandinavian studies on hole-nesters (Sonerud, 1985; Carlson, 1994; Rolstad *et al.*, 2000) and a Lithuanian study on the whole bird communities (Brazaitis and Kurlavičius, 2003), avian responses to VRC have been mostly described in North America where the succession of bird communities may profoundly differ from that in Europe (Helle and Mönkkönen, 1990).

In this paper, we explore avian communities in hemiboreal cut areas in Estonia where, despite the highly varying site-type composition of forest landscapes, timber harvesting has been almost entirely based on clear-cutting (Lõhmus *et al.*, 2004). Similarly, in the recent attempts to improve the consideration of biodiversity aspects, tree-retention techniques (though usually at low levels) have been introduced to all site types (Lõhmus *et al.*, 2006). We therefore had an opportunity to compare the VRC effects on birds in different site types in geographically close areas. We asked (1) which silvicultural characteristics are related to the total abundance and species richness of birds in cut sites; (2) whether the same factors determine the occurrence of harvest-sensitive species groups (hole-nesters and the species of national conservation concern) and (3) whether, and to what extent, do the effects of tree retention depend on forest type.

Materials and methods

Study sites

The study was carried out in 77 pre-thicket cut stands in mainland Estonia, between 57° 36′–59° 18′ N and 24° 39′–27° 50′ E. Estonia is situated in the hemiboreal vegetation zone (Ahti *et al.*, 1968); the mean air temperature is 17°C in July and –6.5°C in January; the average precipitation is 600–650 mm year⁻¹. The terrain is flat. Forests (~50 per cent of the country) do not contain intensive plantations but, due to a long clear-cutting history, the stands are structurally impoverished – usually they have only one even-aged tree layer consisting, on average, of three tree species (Lõhmus *et al.*, 2004, 2005). Approximately 40 per cent of the forests are state owned, having an average growing stock 198 m³ ha⁻¹ (272 m³ ha⁻¹ in mature stands; Adermann, 2004).

The study sites were either random or complete sets of regionally available cuts sampled in the frame of two integrated studies of forestry impacts on biodiversity (Lõhmus, 2006; Lõhmus *et al.*, 2006). Both sampling schemes attempted to include a wide range of productive forest types and varying amounts of post-cut legacies in otherwise similar state-owned cuts in the same regions, and to avoid freshly cut stands. All sites were preselected from geographical information system without previous knowledge on birds. The mean area of the cuts was 3 ha (range 0.4–8 ha); they had been harvested on average 4.9 years (range 2–12 years) prior the study. According to the pre-cut stand, the cuts were classified (according to Lõhmus 1984) into four main types: (1) oligotrophic – nutrient-poor dry *Pinus*-dominated forests (*Cladina*, *Calluna* and *Vaccinium vitis-idaea* types); (2) mesotrophic – mixed forests of *Oxalis* and *Oxalis-Vaccinium myrtillus* types; (3) eutrophic – mostly deciduous forests mixed with *Picea*, belonging to *Aegopodium* and *Filipendula* types; (4) swamp – both mobile- and stagnant-water stands characteristically dominated by *Betula pubescens* and *Alnus glutinosa*, often mixed with *Picea*. Detailed characteristics of the cuts by site types are presented in Appendix 1.

In each cut, the species and diameter at breast height of all live and standing dead trees (including broken-top snags ≥2 m tall) with ≥14-cm diameter as well as the height of snags

were measured. Trunk volumes of the trees were estimated according to species-specific diameter functions (Padari, 2004) used in practical silviculture in Estonia. There were, on average, 11.7 (0–100) live trees per hectare and 3.1 (0–24) dead trees per hectare. Importantly for the interpretation of results, there were relatively few live trees in the swamp cuts found and relatively few standing dead trees in oligotrophic sites (Appendix 1). Of the live trees, 42 per cent were Scots pine (*Pinus sylvestris* L.), 18 per cent birches (*Betula* spp.), 11 per cent European aspen (*Populus tremula* L.) and 13 per cent other rare hardwoods (*Fraxinus excelsior* L., *Ulmus glabra* Huds., *Quercus robur* L. and *Acer platanoides* L.). Of the dead trees, 37 per cent were birches, 22 per cent European aspen, 17 per cent Scots pine, 13 per cent Norway spruce (*Picea abies* L. Karst.) and 8 per cent grey alder (*Alnus incana* L. Moench). The average diameter was 28.8 cm (range 14–84 cm) for live trees and 27.7 cm (14–84 cm) for dead trees; their volumes per hectare were 10.1 m³ (0–74 m³) and 1.2 m³ (0–8.6 m³), respectively.

Oligotrophic sites were regenerating, either naturally or artificially, with Scots pine; the other site types were mostly overgrowing with deciduous trees or had been planted with Norway spruce. To quantify the overgrowth, we (1) directly measured the density and height of all woody plants at least 1 m tall and less than 14 cm in diameter (hereafter, regeneration) in 32 cut sites (24 random 1-m² plots in each site) and, using these as reference values, (2) we classified the regeneration extent visually and using photos in the other cuts. The height was expressed on a five-point scale, after omitting 5 per cent of the tallest plants: 1, <1.2 m; 2, 1.25–1.45 m; 3, 1.5–1.7 m; 4, 1.75–1.95 m; 5, ≥2 m. The numbers of woody plants per square metre were classified as follows: 0, <0.25; 1, 0.25–0.9; 2, 1.0–1.9; 3, 2.0–2.9; 4, 3.0–3.9; 5, ≥4 plants per square metre. (3) Given the correlation between these height and density values ($r_s = 0.44$, $N = 77$, $P < 0.001$), we used their sum (scale 1–10) as the measure of regeneration extent.

Bird counts

Each cut was inventoried in 2004, 2005 or 2006, the cuts of different types, retention levels and age

being well represented in each year (see also Helle and Mönkkönen, 1986, for the weakness of annual fluctuations in clear-cut bird communities). The basic method was a standard two-visit survey: one visit between 10 and 20 May and another between 25 May and 10 June in good weather between sunrise and 11:00 a.m. We additionally visited more than half of the cuts, representing all site types and retention levels, in the evening of the same or preceding day to find previously undetected pairs, nests, etc. In the Estonian old forests, this improved method underestimated true numbers by ~40 per cent, while ~10 per cent of recorded pairs were probably intruders from the surroundings (Lõhmus and Rosenvald, 2005). In cut areas, the biases are probably even smaller, given the lower densities and better visibilities of birds and a distinct species composition, this enabled us to recognize and omit the most likely non-breeders (e.g. tree-dwelling raptors).

In the field, the position of singing males, nests or (in the absence of these) any other observations referring to nesting were recorded on a topographic map (scale 1 : 2000–1 : 3000). The abundance of each species in each site was determined as the maximum count plus probable or confirmed nestings in clearly different locations during the other visit. Territorial birds moving across site borders as well as adult individuals of species with large home range or unstable pairs were counted as 0.5 pairs (Lõhmus and Rosenvald, 2005).

Statistical analysis

We used multivariate regression techniques to explain four characteristics of avian communities: (1) the total density (pairs per hectare); (2) relative species richness (adjusted to area; i.e. residuals of the regression between the logarithm of the cut area and the total species richness); (3) the density of hole-nesters (see Appendix 2) and (4) the occurrence of the species of national conservation concern (according to Eesti Ornitoloogiaühing, 2001; listed in Appendix 2). For the first three variables, we built general linear models; for the latter (binomial) variable, logistic regression was applied. Since clear-cuts without any live or dead retention trees lack any nest sites for hole-nesting birds by definition, this non-habitat was omitted

from the analyses on these birds to distinguish the potential effects of different retention levels.

For model building, we used the procedure of Hosmer and Lemeshow (1989): (1) performed univariate analyses for each explanatory variable, (2) built a preliminary multivariate model, which included the potentially important variables according to univariate analyses; (3) omitted non-significant and/or redundant variables from the multivariate model and (4) checked for interactions between the final set of variables. In the first step, the significance level was set at $\alpha = 0.1$ (to retain variables that could gain significance in combination with other variables); afterwards $\alpha = 0.05$ was used. All analyses were performed with Statistica 6.0 software (StatSoft Inc., 2001).

As explanatory variables, we considered site type (a categorical predictor) and, initially, 13 continuous site characteristics. The latter included six general variables: (1) cut area; (2) cut age; (3) regeneration index (see above); (4) total density of live trees per hectare; (5) species richness of live retention trees and (6) total density of standing dead trees per hectare. The remaining seven variables described tree retention in detail, with a perspective to derive more precise management prescriptions from the analyses: (7) the total trunk volume (m³) of live trees per hectare; (8) the total trunk volume (m³) of dead trees per hectare; (9) density of live conifers per hectare; (10) density of live deciduous trees per hectare; (11) density of live aspens (the most cavity-rich tree species; Remm *et al.*, 2006) per hectare; (12) density of deciduous trees other than aspen per hectare and (13) density of large-diameter (>30 cm) live trees per hectare – given their importance for hole-nesters (Remm *et al.*, 2006).

Redundancy of the explanatory variables was addressed by omitting variables 2, 6, 7 and 10 above first. Cut age (variable 2) was inversely related to the density of live trees ($r_s = -0.57$, $N = 77$, $P < 0.001$) and the volume of dead trees ($r_s = -0.73$, $N = 77$, $P < 0.001$); also, older cuts were larger ($r_s = 0.33$, $N = 77$, $P = 0.004$). One reason for that is the recent change towards more nature-friendly forestry practices: the Estonian Forest Act has required retention of at least 5 m³ ha⁻¹ of live and dead trees during final felling only since 1999. Hence, the real effect of cut age could have been masked by the sample bias and, furthermore, we expected that rather than

cut age itself, bird communities are influenced by overgrowth of the cuts, which was measured separately. The total volumes and densities of trees were strongly correlated (live trees: $r_s = 0.88$, $N = 77$, $P < 0.001$; dead trees: $r_s = 0.93$, $N = 77$, $P < 0.001$); we omitted the volume of live trees and the density of dead trees (variables 6 and 7), as presumably less important for birds, from further analyses. The density of all deciduous trees (variable 10) was omitted due to the strong correlations with its subsets (the densities of aspen and of other deciduous trees) and with large-diameter trees ($r_s = 0.58–0.95$, $N = 77$, $P < 0.001$).

Up to stage (2) of the analysis, we considered all the remaining variables describing tree retention as candidates for alternative models. Most of these variables were intercorrelated but had different ecological meanings, such as the densities and volume of dead retention trees ($r_s = 0.63$, $N = 77$, $P < 0.001$), which pose a common technical problem for assessing their relative biodiversity contributions (Rosenvald and Lõhmus, 2007). Fortunately, the retention variables had no strong correlations ($r_s > 0.4$) with the area and regeneration of the cuts. Finally, since forest type was expectably related to several characteristics of the cuts (Appendix 1), it was kept in multivariate models if it passed the univariate stage (1) to detect additional contributions of structural characteristics. Similarly, the incidence of the species of conservation concern was expected to increase along with the cut area; i.e. the additional explanatory power of other variables was the main interest there.

The assumptions of normality (Kolmogorov–Smirnov test) and the homogeneity of variances (Levene's test) were checked prior to parametric analyses, using square-root or logarithmic transformations in a few appropriate cases (Appendix 1). Given that all continuous variables could not be normalized, we used Spearman rank correlation in the univariate stage (1); this eliminated most of such variables as not significant. The three highly skewed variables (densities of coniferous trees, aspens and other deciduous trees) that passed stage (1) were introduced into general linear models alternatively in their non-normal continuous form and as categorical variables (after grouping the values) – in neither case none of these variables reached final multivariate models. For univariate tests of forest-type effects, we used

one-way analysis of variance (ANOVA) or, in non-parametric cases, Kruskal–Wallis ANOVA.

Results

Among the total of 620.5 pairs of 61 bird species, there were 57.5 pairs (9 per cent) of 13 species of hole-nesters and 33 pairs (5 per cent) of nine species of national conservation concern (Appendix 2). The total bird densities were explained with two alternative models, both of which included site type (highest densities in swamp sites, lowest in oligotrophic sites; Figure 1a) and contained no significant interaction terms (Table 1). The first model (model I, Table 1) revealed the bird density increase along with dead-tree volume (Figure 2a; the abundances have been grouped for illustrative purposes). Alternatively, model II showed that smaller cuts had higher bird densities (Table 1).

The relative avian species richness was a function of site type (oligotrophic sites poorer than the others; Figure 1b), dead-tree volume (Figure 2b) and more tree species on the cuts (Table 1). Again, no significant interaction between any of these variables appeared. Significant positive univariate effects were recorded also for the densities of all live trees, large-diameter live trees and deciduous trees other than aspen (Appendix 1).

The density of hole-nesters in the 53 retention cuts was explained by two alternative univariate relationships with variables dependent on each other (Table 1; Appendix 1). The influence of site type contained a significant contrast between mesotrophic and oligotrophic sites (Figure 1c). The positive effect of tree-species richness disappeared when forest type was taken into account. Hole-nester density co-varied weakly, but reliably, with the density of all other species on the 53 retention cuts ($r_s = 0.27$, $P = 0.048$) and with the relative species richness of these species groups ($r_s = 0.28$, $P = 0.042$).

The species of national conservation concern nested in 25 cuts of the 77 (32 per cent); preferably (multivariate model: log-likelihood = −42.5, $P = 0.002$) in larger cuts (coefficient 0.34 ± 0.17; $\chi^2_1 = 4.3$, $P = 0.038$) with higher densities of live trees (coefficient 0.06 ± 0.02; $\chi^2_1 = 9.0$, $P = 0.003$; Figure 3). In the univariate stage, statistically significant positive effects were also detected for the density of coni-

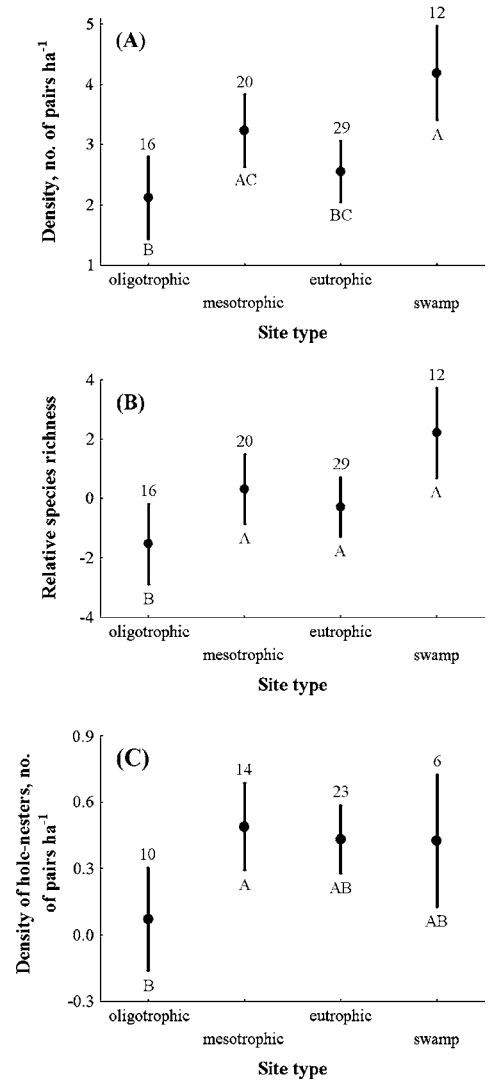

Figure 1. Mean density of birds (a), relative number of bird species (b) and mean density of hole-nesters (c) according to the site types of cuts (95% confidence interval). The numbers above the bars are sample sizes; the letters below denote statistical similarity (means followed by the same letter means no difference in general linear model at $\alpha < 0.05$; see Table 1 for the models).

Table 1: General linear models explaining the density of all birds and their relative species richness (adjusted to area) in 77 cuts and the density of hole-nesters in 53 retention cuts

Model and variable	Coefficient (mean ± standard error)	F	P
Density, no. of pairs per hectare			
I. $R^2 = 0.25$, $F = 6.0$, $P < 0.001$			
Site type		6.47	<0.001
Volume of dead trees per hectare	0.61 ± 0.27	5.29	0.024
II. $R^2 = 0.25$, $F = 6.0$, $P < 0.001$			
Site type		5.21	0.003
Area	−0.23 ± 0.1	5.10	0.027
Relative species richness ($R^2 = 0.35$, $F = 7.6$, $P < 0.001$)			
Site type		5.38	0.002
No. of tree species	0.31 ± 0.13	6.16	0.015
Volume of dead trees per hectare	1.31 ± 0.54	5.89	0.018
Density of hole-nesters, no. of pairs per hectare			
I. Site type ($R^2 = 0.16$, $F = 3.1$, $P = 0.037$)		3.05	0.037
II. No. of tree species ($R^2 = 0.11$, $F = 6.1$, $P = 0.017$)	0.24 ± 0.1	6.11	0.017

Note that there are two alternative models (referred to by Roman numerals) for the density of all birds and the density of hole-nesters.

fers, large-diameter trees and the tree-species richness (Appendix 1). The incidence of the species of conservation concern was related to higher relative species richness of all birds (likelihood-ratio test of logistic regression: $\chi^2_1 = 8.9$, $P = 0.003$), hole-nester density ($\chi^2_1 = 5.0$, $P = 0.026$) and hole-nester species richness ($\chi^2_1 = 7.1$, $P = 0.008$), but not to the total density of birds ($\chi^2_1 = 1.7$, $P = 0.188$).

Discussion

We found that tree retention influenced birds independently of forest type but the effects differed for the whole communities and the harvest-sensitive species groups. Even though the latter tended to prefer the cuts having the densest and most species-rich avian communities, that co-variation was too weak to justify the use of general community characteristics (particularly density) as universal shortcuts of forestry impacts on bird biodiversity. Unfortunately, most threatened species, again, are so rare, often elusive and laborious to detect (Imbeau *et al.*, 2001) that their absence is uninformative at the stand scale. Thus, forest managers usually only assume that some particular habitat modifications

(e.g. the retention of adequate legacies) would increase the probability of such species' presence.

In this study, we were able to demonstrate the stand-scale relevance of VRC: the incidence of species of national conservation concern clearly depended on live-tree retention (see also Conner *et al.*, 1991; Niemi and Hanowski, 1997). This effect could not be explained with the type-related bias in retention levels (see Materials and Methods) since these species were well dispersed between different site types (no site-type effect). In Finland, e.g. threatened bird species are mostly restricted to and may have value as management indicators only in fertile forests (Similä *et al.*, 2006). Yet, it is unclear to what extent each stand-scale retention would influence the viability of the populations; the latter is revealed only at the landscape scale (Angelstam *et al.*, 2004a) and rather in demography and long-term trends than absolute densities. For those laborious assessments, focal taxa should be selected (Angelstam *et al.*, 2004b), so the question is how to distinguish VRC-dependent species.

Resident hole-nesters have been considered suitable targets of sustainable forestry in boreal regions: they suffer seriously from modern timber extraction (Schmiegelow *et al.*, 1997; Imbeau *et al.*, 2001) and obviously cannot nest
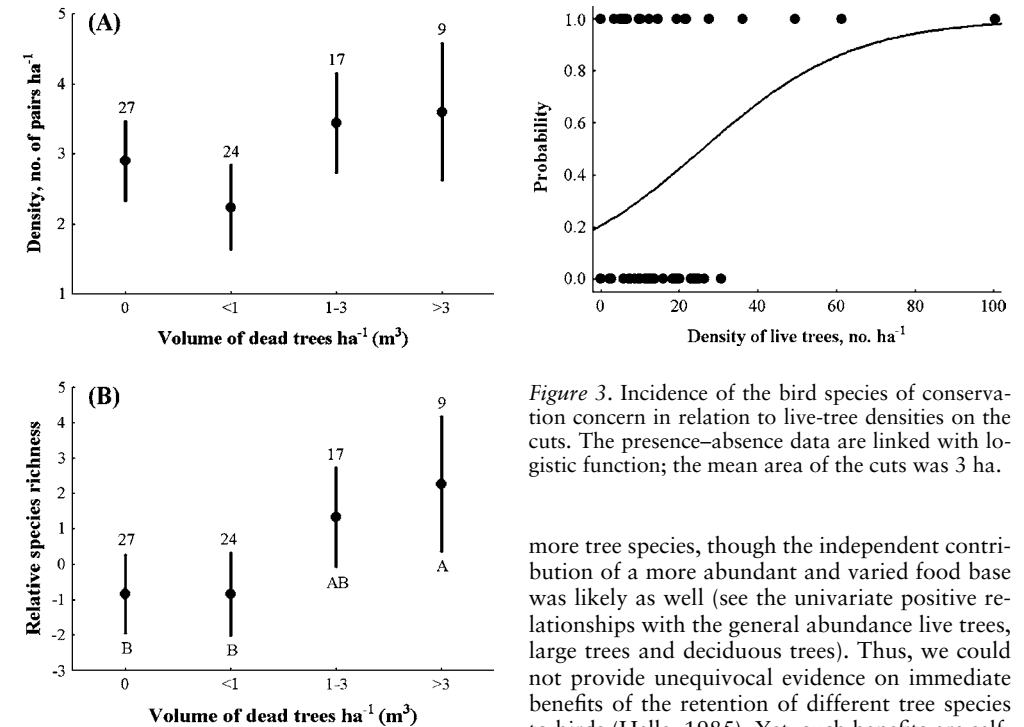
Figure 2. Mean density of birds (a) and relative number of bird species (b) according to the volume of dead trees on the cuts (95% confidence interval). The numbers above the bars are sample sizes; the letters below denote statistical similarity (means followed by the same letter were not different in ANOVA at α < 0.05).

Figure 3. Incidence of the bird species of conservation concern in relation to live-tree densities on the cuts. The presence–absence data are linked with logistic function; the mean area of the cuts was 3 ha.

on treeless cuts. However, we were not able to detect any further relationships between tree retention and the abundance of hole-nesters, though their share in the bird communities exceeded the average for European forests (5 per cent; Newton, 1998). The common pattern behind the two alternative models explaining their densities on retention cuts (via site-type or tree-species richness, respectively) was probably that the bird-poor (Figure 1c) oligotrophic cuts usually had only Scots pines, which contain few cavities at the age of cutting. The increased incidence of hole-nesters may partly explain the higher relative species richness of all birds in the cuts with

more tree species, though the independent contribution of a more abundant and varied food base was likely as well (see the univariate positive relationships with the general abundance live trees, large trees and deciduous trees). Thus, we could not provide unequivocal evidence on immediate benefits of the retention of different tree species to birds (Helle, 1985). Yet, such benefits are self-evident for tree-specific epiphytes and invertebrates and – as a source of structural complexity of the stand (Zenner, 2000) – tree-species richness should enhance the bird diversity in the next forest generation as well (Hansen *et al.*, 1995).

The recorded site-type effects on bird abundance, species richness and the abundance of hole-nesters followed the well-known increases along with the habitat productivity (Helle and Mönkkönen, 1990) and moisture gradients (Haapanen, 1965). Importantly, however, the lack of interactions between site type and the variables of tree retention contrasts with the common assumption that biotic communities are adapted to natural disturbances, which, therefore, should be mimicked by forest managers (Fries *et al.*, 1997; Angelstam, 1998). It is unlikely that the observed benefits of standing dead trees – a characteristic element of naturally burnt areas – on birds could result from such adaptations (Schieck and Song, 2006), as the volumes of retained dead trees in our study were less than 1 per cent of those reported after natural burns (Siitonen,

2001). Furthermore, the dead-tree effects were detected for general bird abundance and species richness only, and not for hole-nesters that actually nest there. Thus, biologically the co-variation of dead-tree retention and general bird community characteristics is difficult to explain (but see Schulte and Niemi, 1998; Simon *et al.*, 2002, for similar results).

On the other hand, one should not make too far-reaching conclusions from the lack of proof for the adaptation assumption in our study. First, birds in general may tolerate forestry operations better than many other taxa (Imbeau *et al.*, 2001), particularly at small scales (Similä *et al.*, 2006). Second, even though birds could guide disturbance-based management at the landscape scale (Angelstam *et al.*, 2004b), they may be less informative in heterogeneous landscapes. In our naturally mosaic hemiboreal forests, the avian communities in the patches of contrasting forest types responded similarly to management; thus, it is unlikely that patch-specific management would make a difference at the large scale. One reason for this may be the scarcity of bird species (such as *Lullula arborea* and *Caprimulgus europaeus*) adapted to large stand-replacing disturbances in hemiboreal Europe. Third, the low retention levels of our study (mostly up to 5 per cent of growing stock) may not mimic natural disturbances sufficiently well – an explanation provided by Virkkala (2004) for a lack of retention effects on Finnish birds. On average, significant differences from clear-cuts in the abundance and species richness of various taxa appear at green-tree retention levels over 15 per cent of the growing stock (Rosenvald and Lõhmus, 2007) and over 10 per cent may be needed for many tree-dwelling bird species in northwestern North America (Norton and Hannon, 1997; Schieck and Song, 2006). Moreover, it is critical to distinguish between the failures to mimic disturbances and to retain the conditions for closed-forest species as the latter is not the primary aim of VRC (Franklin *et al.*, 1997). To summarize, the explicit planning of VRC could greatly benefit from future studies similar to our's on taxa other than birds, in homogeneous *vs* heterogeneous landscapes and on biodiversity responses to real natural disturbances having varying amounts of legacies left.

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Appendix 1: Cut characteristics by site types (median; quartile range in brackets) and their univariate relationships with bird community characteristics

Cut variable	Site type[α]				Bird community characteristics[β]			
	Oligotrophic (N=16)	Mesotrophic (N=20)	Eutrophic (N=29)	Swamp (N=12)	Total density	Relative species richness	Hole-nester density[γ]	SPEC[δ]
Site type					‡	‡	†	
Regeneration	3 (1; 3)[B]	4 (3; 5)[AB]	4 (3; 5)[A]	4 (3; 5.5)[A]	0.10	−0.01	−0.02	*
Area (ha)	2.6 (1.9; 3.7)	2.7 (1.8; 3.2)	3.3 (2.3; 4)	2.4 (2.1; 3)	−0.26†	−0.05	0.02	*
Live trees (no. per ha^{-1})	9.9 (0; 13.7)	11.8 (0; 17.1)	9.7 (4.9; 19.3)	2.7 (0; 7.4)	0.13	0.25†ε	0.14	‡
Dead trees (m^3 per ha^{-1})	0 (0; 0.6)	0.7 (0; 2)	1.2 (0.2; 2)	0 (0; 0.7)	0.20*π	0.35‡π	0.34†π	
Live trees (d.b.h. >30 cm; no. per ha^{-1})	2.6 (0; 8.1)[AB]	6.6 (1; 12.4)[A]	3.1 (0.9; 6.7)[AB]	0.2 (0; 1.9)[B]	0.17	0.26†ε	0.19	
Conifers (no. per ha^{-1})	6.7 (0; 13.1)	4.2 (0; 10.6)	0 (0; 0.5)	1 (0; 4.6)	0.12	0.17	−0.06	
Aspen (no. per ha^{-1})	0 (0; 0)	0 (0; 2.5)	0 (0; 1.9)	0 (0; 0)	0.01	0.21*	0.21	
Deciduous trees, excluding aspen (no. per ha^{-1})	0.1 (0; 1.4)[a]	0.8 (0; 3.6)[ab]	5.7 (2.2; 12.2)[b]	0.2 (0; 2.1)[ab]	0.17	0.31‡	0.24*	
No. of tree species	2 (2; 3)[B]	3 (2; 6)[AB]	4 (3; 6)[A]	3 (3; 4)[AB]	0.15	0.36‡	0.40†‡	†

[α] Means followed by the same letter are not different at $\alpha < 0.05$ according to ANOVA (uppercase letters) or Kruskal–Wallis ANOVA (lowercase letters).
[β] Numbers are Spearman rank correlation coefficients; site-type effects were tested with ANOVA; the relationships for the species of conservation concern were tested in logistic regression (log-likelihood test); P values: *<0.1, †<0.05, ‡<0.01.
[γ] Only cuts with residual trees.
[δ] Species of national conservation concern (Eesti Ornitoloogiaühing, 2001).
[ε] Square-root-transformed for further analyses.
[π] Log-transformed for further analyses.

Appendix 2: Bird species abundance (pairs per hectare) according to forest type and live-tree abundance groups

Bird species (total no. of pairs)	Oligotrophic				Mesotrophic				Eutrophic				Swamp			
	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20
Anas platyrhynchos (3)	0	0	0	0	0.04	0	0	0	0	0.03	0.04	0	0	0	0	0
Falco subbuteo (1)	0	0	0.07	0.09	0	0	0	0	0	0	0	0	0	0	0	0
Tetrao tetrix (1)*	0	0	0	0.09	0	0	0	0	0	0	0	0	0	0	0	0
Bonasa bonasia (1)*	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0
Grus grus (1)*	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0.25	0.39
Tringa ochropus (4.5)	0.03	0	0	0	0	0	0	0.05	0.06	0	0	0	0.03	0.10	0.25	0.39
Scolopax rusticola (1)	0	0	0	0	0	0.08	0.03	0	0	0	0	0	0	0	0	0
Gallinago gallinago (22.5)	0.06	0	0	0	0.09	0	0.06	0	0.09	0.19	0.07	0.14	0.26	0.10	0.51	0
Columba palumbus (0.5)	0	0	0.07	0.05	0	0	0	0	0.02	0.02	0.07	0.07	0	0	0	0
Cuculus canorus (5)	0	0	0.07	0	0	0	0	0.05	0	0	0	0	0	0	0	0
Caprimulgus europaeus (2)*	0	0.16	0	0	0	0	0	0.05	0	0	0	0	0	0.05	0	0
Dryocopus martius (7)*†	0	0	0	0	0	0.08	0.03	0.10	0	0.03	0.07	0.11	0	0	0	0
Picus canus (3.5)*†	0	0	0	0	0	0.16	0.06	0	0	0.03	0.02	0.07	0	0.05	0	0
Dendrocopos major (12)†	0	0	0	0.05	0	0.08	0.16	0.10	0	0.06	0.11	0	0.06	0.10	0	0
Dendrocopos leucotos (1)*†	0	0	0	0	0	0	0	0	0	0	0.04	0.11	0.09	0.15	0	0
Dendrocopos minor (1)†	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0	0	0
Lullula arborea (5)*	0.06	0.10	0.13	0.09	0	0	0	0	0	0	0	0	0.4	0.51	0	0
Anthus trivialis (99)	0.37	0.42	0.53	0.70	0.24	0.66	0.53	0.63	0.24	0.34	0.41	0.61	0.03	0.51	0.51	0.39
Motacilla alba (5.5)	0.06	0.05	0	0	0	0	0.16	0.10	0.02	0.02	0.09	0	0.03	0.10	0	0
Troglodytes troglodytes (8.5)	0	0	0.03	0	0	0	0.09	0.10	0.04	0	0	0.11	0	0.10	0	0
Prunella modularis (5)	0	0	0	0	0	0	0.13	0.10	0.04	0	0	0	0.06	0.10	0	0
Erithacus rubecula (11)	0.06	0	0.03	0	0.07	0.08	0	0.10	0	0	0.04	0.11	0.09	0.21	0	0.19
Phoenicurus phoenicurus (1.5)†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saxicola rubetra (4.5)	0.12	0	0	0	0.04	0	0.03	0.03	0.06	0.05	0	0	0.06	0.10	0	0
Turdus merula (11)	0	0	0	0	0.07	0.08	0.03	0.16	0	0.03	0	0	0.03	0.31	0.25	0
Turdus pilaris (1.5)	0	0	0.03	0	0	0	0	0	0	0	0	0	0	0.05	0	0
Turdus iliacus (1.5)	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0.05	0	0
Turdus philomelos (7.5)	0	0	0	0	0.04	0.08	0.03	0.03	0.04	0.05	0	0	0.06	0.15	0	0
Turdus viscivorus (3)	0	0.05	0.07	0.14	0	0	0.03	0.03	0.02	0	0	0	0	0	0	0
Locustella fluviatilis (10.5)	0	0	0	0	0.04	0	0.06	0.06	0	0	0.07	0.14	0.20	0.10	0	0

Appendix 2: Continued

Bird species (total no. of pairs)	Oligotrophic				Mesotrophic				Eutrophic				Swamp			
	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20
Locustella naevia (4)	0	0	0	0	0	0	0	0	0.04	0	0.04	0	0	0.21	0	0
Acrocephalus schoenobaenus (1.5)	0	0	0	0.09	0	0	0	0	0	0	0	0	0.09	0	0	0
Acrocephalus dumetorum (5.5)	0	0	0	0	0	0	0	0	0.09	0	0.09	0	0	0.10	0	0
Acrocephalus palustris (1)	0.06	0	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0
Sylvia borin (46.5)	0.06	0	0.10	0	0.48	0.16	0.06	0	0.58	0.08	0.20	0.11	0.17	0.51	0	0
Sylvia curruca (5)	0	0	0	0.09	0.02	0	0	0	0.04	0	0	0	0.09	0.10	0	0
Sylvia communis (93.5)	0.06	0	0.13	0	0.84	0.08	0.31	0.21	0.73	0.19	0.59	0.18	0.81	0.67	0.51	0.39
Sylvia atricapilla (6)	0	0	0.03	0	0.04	0	0	0.10	0.02	0	0.06	0.07	0.03	0	0	0
Phylloscopus sibilatrix (3.5)	0	0	0.03	0.09	0	0	0	0	0	0	0	0	0	0.21	0	0
Phylloscopus trochilus (67)	0.46	0	0.10	0.28	0.44	0.16	0.22	0.68	0.39	0.02	0.17	0.22	0.46	0.82	0	0
Phylloscopus collybita (20.5)	0	0	0.03	0	0.18	0.16	0.16	0.21	0	0.05	0.15	0.32	0	0	0.76	0.39
Ficedula hypoleuca (3.5)†	0	0	0	0	0	0.16	0	0.10	0	0	0.06	0	0	0	0	0
Muscicapa striata (1.5)†	0	0	0	0.09	0	0	0	0	0	0	0.06	0	0	0	0	0
Parus montanus (3.5)†	0	0	0	0.09	0	0	0.03	0	0	0.02	0.02	0.04	0	0.10	0	0
Parus caeruleus (0.5)†	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0.10	0	0
Parus major (20)†	0	0	0	0	0.02	0	0.16	0.10	0	0.14	0.30	0.14	0.03	0.10	0.51	0
Aegithalos caudatus (1.5)	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0
Sitta europaea (1)†	0	0	0	0	0	0	0	0.10	0	0	0.06	0.04	0	0	0	0
Certhia familiaris (2)†	0	0.10	0	0	0	0	0	0	0	0	0.06	0.04	0.17	0.10	0	0.39
Lanius collurio (10.5)*	0	0.10	0	0	0	0	0	0	0.04	0.03	0.09	0	0.17	0.10	0	0
Oriolus oriolus (1)	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0
Garrulus glandarius (1)	0	0	0	0	0	0.08	0	0	0	0	0	0.04	0	0	0	0
Corvus corax (2.5)	0	0	0.07	0	0	0	0.09	0	0	0	0	0	0	0	0	0
Fringilla coelebs (30.5)	0.09	0.26	0.20	0.47	0.02	0	0.28	0.47	0.02	0.02	0.11	0.22	0.10	0.10	0.25	0.19
Carduelis spinus (2)	0	0	0	0	0	0	0.06	0	0	0.03	0	0	0	0	0	0
Carduelis carduelis (1)	0	0	0.07	0	0	0	0	0.05	0	0	0	0	0	0	0	0
Pyrrhula pyrrhula (8)	0	0	0.03	0.05	0	0.16	0.06	0.05	0.02	0	0.06	0.11	0	0.10	0	0
Carpodacus erythrinus (28.5)	0.03	0	0.07	0	0	0.16	0.06	0.10	0.24	0.08	0.35	0.07	0.17	0.26	0	0
Loxia curvirostra (1)	0	0	0	0	0	0	0	0.05	0	0	0.02	0	0	0	0	0
Emberiza citrinella (3)	0.06	0.05	0.07	0	0	0	0	0	0.03	0.03	0	0	0	0.10	0	0
Emberiza schoeniclus (2.5)	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0.10	0	0

IV

Appendix 2: *Continued*

Bird species (total no. of pairs)	Forest type and retention level (no of live trees per hectare)															
	Oligotrophic				Mesotrophic				Eutrophic				Swamp			
	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20	0	<10	10–20	>20
Clear-cut characteristics																
No. of cuts	6	2	5	3	6	3	7	4	6	9	9	5	6	4	1	1
Total area of cuts	16.4	9.5	15.1	10.8	22.7	6.1	16.0	9.6	23.2	31.0	27.0	13.9	17.3	9.8	2.0	2.6
Bird community characteristics																
Total density (pairs per hectare)	1.52	1.15	1.79	2.28	2.69	2.30	2.94	3.71	2.87	1.58	3.56	2.92	3.37	5.35	3.54	2.33
Species richness	13	7	18	13	16	15	25	22	21	23	32	20	20	25	8	7
Hole-nester density (pairs per hectare)	0	0	0	0.23	0	0.49	0.44	0.57	0	0.32	0.70	0.40	0	0.41	0.51	0
Density of species of conservation concern (pairs per hectare)	0.06	0.37	0.13	0.19	0	0.25	0.09	0.16	0.04	0.10	0.26	0.11	0.17	0.26	0	0.39

* Species of national conservation concern.
† Hole-nester.

Short-term determinants and long-term prospects of retention-tree survival in hemiboreal cut areas

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Abstract.
Survival of live retention trees is a key issue for stand-scale applications of natural-disturbance-based silviculture. In 2002–2007, we explored post-cut survival of 3255 trees in 102 cut areas in Estonia, focusing on long-term survival prospects, pre-adaptation of the trees and spatial variation in survival. Wind damage comprised 89.6% of tree deaths. In one subsample, the number of live trees decreased 35% in six years, in another – 36% in five years, adding 4.4 m^3 of downed dead trunks and 1 m^3 of standing dead trees ha^{-1} in both cases. Yet, the annual rates of natural mortality declined in time, and 29–38% of the trees were estimated to be alive after 40 years (22–29% after 100 years). According to multilevel logistic regression, the main determinants of survival were tree species (best in hard deciduous trees – *Fraxinus, Ulmus, Quercus, Acer, Prunus* and *Sorbus*) and diameter (species-dependent effects), tree position relative to forest edge (best near current or former forest edge), post-harvest density of trees (positive), and exposure (negative). The results implied that: (1) green-tree retention can effectively increase the abundance of large shade-tolerant trees, but it is equally important for producing coarse woody debris; (2) larger individuals, interior forest trees near existing forest edges and pre-adapted trees in open conditions should be preferably retained; (3) in terms of tree survival, differentiating tree-retention geographically or amongst site types is not justified. The critical question for future research is the necessary abundance of old trees in the next forest generation.

Key words: coarse woody debris, green tree retention, forest management, variable retention cutting, windthrow

Introduction

Variable retention cutting (VRC) is the main stand-scale application of the developing natural-disturbance-based silviculture, which, by emulating the consequences of natural stand-replacing disturbances, aims at better consideration of biodiversity in forest management (Franklin et al. 1997; Drever et al. 2006). Though its basic technique – permanent retention of live trees ("green-tree retention") at cutting – obviously has a general positive effect on forest biota (Rosenvald and Lõhmus 2007a), the practical guidelines are still poorly elaborated and supported by field data. Partly, this is due to the complex interplay between immediate and future value of the trees (Lõhmus et al. 2006). Immediate effects of tree-retention on the cuts are seen, for example, for threatened saproxylic beetles adapted to post-disturbance conditions (Martikainen 2001), while future values are more important for epiphytic forest bryophytes that tend to go extinct on solitary trees (Lõhmus et al. 2006) but can re-establish old trees in the young forest (Lõhmus and Lõhmus 2007). Such a re-establishment is impossible if the trees die earlier; however, the deaths also provide essential coarse woody debris for saproxylic forest species (Junninen et al. 2007).

Thus the survival of the live retention trees is a key knowledge for VRC but, despite the at least 20 studies performed so far (Rosenvald and Lõhmus 2007a), there are major gaps inhibiting its effective application. Notably, long-term survival prospects of the trees remain unknown but are suspected to be low (e.g., Jull 2001; Busby et al. 2006), mostly due to the extra wind damage caused by the increased post-cut exposure of the trees (Foster 1988; Ruel et al. 2003). However, the dropped average survival rates may start increasing again along with the selective mortality of the most susceptible trees (Scott and Mitchell 2005; Busby et al. 2006). Furthermore, the individuals of at least some species may also adapt to these more open conditions by accelerating their diameter growth (Holgen et al. 2003; Jakobsson and Elfing 2004), strengthening their root system (Foster 1988; Peterson 2004) and changing their canopy shape (Foster 1988; see also Canham et al. 2001). These processes may be addressed by two complementary retention strategies: (1) given that interior forest trees are particularly susceptible to opening up the forest (e.g., Lohmander and Helles 1987; Foster 1988; Peltola 1996; Talkkari et al. 2000) – to prefer the pre-adapted trees at the edges of former openings; (2) to reduce per capita mortality rates by increasing retention densities to the levels where the trees provide shade for each other (Scott and Mitchell 2005; Busby et al. 2006).

Secondly, retention-tree survival may vary in space, which questions the attempts to introduce similar retention techniques to all site types (Rosenvald and Lõhmus 2007b). On the one hand, given the differences between natural disturbance regimes amongst site types (e.g., Angelstam 1998; Lõhmus et al. 2004) and geographic regions (Bergeron et al. 2002; Lorimer and White 2003), their dominating tree species may differ in the resilience to abrupt changes in microclimate caused by cutting (Valinger and Fridman 1999; Lanquaye-Opoku and Mitchell 2005). On the other hand, depending on soil moisture and depth, even relatively wind-resistant tree species may be locally vulnerable (Peterson 2004) suggesting, for instance, that in wet forests alternative management techniques to VRC should be considered (Valinger and Fridman 1999).

In this paper, we explore the process and determinants of post-cut survival of live retention trees in hemiboreal cut areas in Estonia, with an emphasis on the pre-adaptation and spatial aspects as well as the prospects of long-term survival. In terms of pre-adaptations, we expect that the trees growing near pre-cut edges survive better; we also explore the differences between tree species and size classes. As for spatial aspects, we test whether the survival differs between geographic regions and site types (being higher on moist mineral soils where stable root hold can be established; Schaetzl et al. 1989; Ray and Nicoll 1998) and depends on post-cut shade provided by forest edges or other retention trees. Based on the mean annual survival, its variance and trends (the possible temporal increase), we discuss the prospects of the retention trees to reach the next forest generation. Finally, we list the implications of our study for forest managers and the needs for future studies.

Material and Methods

Study Areas

The study was carried out in four randomly selected state forest districts in three Estonian regions located at 58°–59°N and 25°–27°E (Figure 1). Estonia is situated in the hemiboreal vegetation zone (Ahti et al. 1968). The mean air temperature is 17 °C in July and –6.5 °C in January; the average precipitation is 600–700 mm per year. Forests (ca. 50% of the country) do not contain intensive plantations but 25% are drained and, due to a long clear-cutting history, the stands are structurally impoverished

– usually they have only one even-aged tree layer consisting, on average, of three tree species (Lõhmus et al. 2004; 2005). Approximately 40% of the forests are state-owned, having an average growing stock 198 m³ ha⁻¹ (272 m³ ha⁻¹ in mature stands; Adermann 2004).

All studied districts comprised large, but extensively managed, forest areas on flat terrain below 75 m a.s.l. The study included all the 102 stands that had been harvested in 2001 (69 cut areas with 2157 retention trees; 70% in Laeva and Alatskivi regions) and winter-early spring 2002 (33 cut areas with 1107 trees; 73% in Viljandi region). The mean area of the cuts was 3 ha in the Laeva and Alatskivi districts and 1.5 ha in the Viljandi region (total mean 2.3 ha; range 0.3–6.9 ha). Age of the pre-cut stands had been mostly 50–80 (max. 110) years for deciduous stands and 90–110 (max. 180) years for conifer stands. According to the pre-cut stand, the cuts were classified into four main types on the soil moisture and fertility gradients (following Lõhmus 1984): (1) oligotrophic – nutrient-poor dry *Pinus*-dominated forests of *Vaccinium vitis-idaea* and *V. myrtillus*-types (8 cuts/104 trees; only in Viljandi region); (2) mesotrophic – mixed forests of *Oxalis*, *Oxalis-Vaccinium myrtillus* and *Hepatica*-types (25/508; dominating in the Viljandi region); (3) eutrophic – mostly deciduous forests mixed with *Picea*, belonging to *Aegopodium*- and *Filipendula*-types (58/2376; dominating in Laeva and Alatskivi); (4) swamp – both mobile- and stagnant-water stands, usually with some drainage effects (12/276).

A total of 16 tree species had been retained on the cuts. To reach meaningful sample sizes (see Table 1), only three of these were considered at the species level for most analyses: European aspen (*Populus tremula* L.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.). The Silver birch (*Betula pendula* Roth.) and Downy birch (*B. pubescens* Ehrh.), which commonly hybridize, were treated at the genus level. The remaining deciduous trees were separated into two groups: (a) soft deciduous trees – Small-leaved lime (*Tilia cordata* P. Mill.), Black alder (*Alnus glutinosa* L. Gaertn.), Grey alder (*A. incana* L. Moench) and Goat willow (*Salix caprea* L.); (b) hard deciduous trees – Common ash (*Fraxinus excelsior* L.), Mountain elm (*Ulmus glabra* Huds.), European white elm (*U. laevis* Pall.), Common oak (*Quercus robur* L.), Norway maple (*Acer platanoides* L.), Bird-cherry (*Prunus padus* L.) and Mountain ash (*Sorbus aucuparia* L.). Species composition differed between the study districts (Appendix); most notably, 83% of pines were in Viljandi region and 94% of hard deciduous trees in Laeva and Alatskivi districts.

Fig. 1 Locations of the studied forest districts: (1) Viljandi (Kabala and Kõpu districts), (2) Laeva and (3) Alatskivi region

Table 1 Retention numbers, tree sizes (trunk volumes), and the mortality of different species during the study. Statistical estimates based on less than five observations are given in parentheses.

Tree species	Retained trees		No. of trees that died during the study				Wind-caused deaths, %
	No.	Tree volume, m³ (mean ± SD)	To-tal	Up-rooted	Trunk bro-ken	Died stand-ing	
Populus tremula	461	2.34 ± 1.67	214	99	91	24	89
Betula spp.	1028	0.82 ± 0.55	449	316	89	44	90
Pinus sylvestris	647	0.97 ± 0.65	277	234	34	9	97
Picea abies	47	0.59 ± 0.63	20	15	2	3	85
Tilia cordata	232	0.43 ± 0.38	84	84	0	0	100
Salix caprea	24	0.36 ± 0.28	9	5	3	1	89
Alnus glutinosa	107	0.69 ± 0.65	10	2	6	2	82
Alnus incana	31	0.31 ± 0.19	12	5	6	1	92
Fraxinus excelsior	576	0.54 ± 0.55	57	22	0	35	39
Ulmus spp.	31	0.35 ± 0.19	0	0	0	0	(0)
Quercus robur	32	0.64 ± 0.5	1	1	0	0	(100)
Acer platanoides	33	0.87 ± 1.03	4	4	0	0	(100)
Prunus padus	2	(0.39± 0.07)	1	0	1	0	(100)
Sorbus aucuparia	4	(0.22± 0.14)	1	0	1	0	(100)
Total	3255	0.96 ± 1.0	1139	787	233	119	89.6

Field methods

In spring 2002, all live (incl. seed trees, which often were inseparable from the trees retained for biodiversity only) and standing dead trees (incl. broken-top snags >2 m tall) with diameter at breast height (DBH) ≥14-cm were mapped in the field; their species, DBH (also height for snags) and condition were recorded. Trunk volumes of the live and dead trees were estimated according to species-specific diameter-functions (Padari 2004) used in practical silviculture in Estonia. Every next summer until 2007, the survival, type of damage if present, and (in case of snags) any changes in height of each tree were examined. The causes of tree death were classified as windthrow, trunk breakage at foot, trunk breakage creating a snag, or desiccation. Among 51 broken-trunk trees having live branches left, we subjectively considered four trees broken below 4 m as dead, and the taller ones as alive.

Exposure of individual trees to wind was described using three standard variables: (1) FETCH – the sum of distances (m) to the nearest forest edges for eight cardinal directions, measured from aerial photographs. Distances over 300 m were not further measured (Scott and Mitchell 2005), i.e. the maximum sum was 2400 m; (2) DIREX – a simplified version of FETCH (Scott and Mitchell 2005) indicating the number (1...8) of cardinal directions with the nearest forest edge over 30 m away (DIREX30), 60 m (DIREX 60) or 90 m (DIREX 90); (3) tree position relative to various edges (defined as a distance up to 20 m) – either at the edge of (a) a field or meadow; (b) a road (at least 15 m wide); (c) a forest; (d) an earlier cut area (regeneration height up to 10 m) or (e) in the cut interior. In addition, given that western winds predominate in Estonia, we calculated modified FETCH (hereafter FETCHw) using only three western directions (SW, W, NW) to analyze whether a region-specific approach might be preferred to the standard variable.

Statistical analysis

From all analyses, we omitted the nine retention trees that were cut during the study. The post-cut survival was considered separately in the cuts of 2001 (data for six years) and 2002 (five years) for their particular post-cut years represented different calendar years. To check for a possible temporal decrease in the annual tree-mortality on the cuts, we performed a general linear analysis with these two „cohorts" as a categorical factor and post-cut year as the continuous variable.

For rough projection of the retention-tree population, we modelled the annual post-cut mortality as decreasing (see Results) linearly from our estimates of the 1st year mortality of the two „cohorts" to the mortality rates of large (DBH >20 cm) managed-forest trees, and stabilizing at that level. The data on forest trees had been collected in two permanent plots in Estonia (Kiviste et al. 2005). In one plot, 14,541 trees had the mean annual mortality 0.46% for natural causes and 1.23% when thinning added; in the second, the rates for 5,088 trees were 0.45% and 1.04%, respectively. We calculated four scenarios to illustrate the influence of different assumptions and to capture the real values at greater probability: (1) maximum survival with natural mortality only – the best survival estimates for both retention trees and forest trees, assuming that that a stable survival typical to forests will be reached in 30 years (see Lõhmus et al. 2004 for a similar assumption); (2) minimum survival with natural mortality only – the worse survival estimates and a duration of 40 years to stabilize; (3) maximum and (4) minimum survival with thinnings – similar to scenarios (1) and (2), respectively, except that the survival of forest trees included the cuttings.

For analysing the survival of individual trees, we used multivariate logistic regression with hierarchical data structure (Alenius et al. 2003): three geographical regions (level 1) included the 102 cuts (level 2) with the total of 3255 trees (level 3). The data were analysed by fitting mixed generalized linear models (SAS PROC GLIMMIX); the levels were taken into account using Kenward-Roger method for determining denominator degrees of freedom (Littell et al. 2002). The dependent variable was the survival (1, live; 0, dead) of the tree by the end of the study period (after 5–6 post-cut years, depending on cutting year). Initially, eleven independent variables were considered (Table 2) but the approach was simplified by omitting two non-significant and four redundant variables (see below). Notably, the geographical region (identifier of level 1) was omitted as non-significant (see Results); thus the final model comprised only two levels and a random intercept.

Variable redundancy was a significant problem for exposure variables and tree species, which could not be omitted prior to analyses due to their expected biological relevance. At the tree level, diameter was independent

of all exposure variables; its dependence on tree species (see Table 1 and Appendix) was addressed by nesting the diameter within species. This approach (1) is more realistic than a common across-species quantitative relationship between tree size and survival probability, (2) allowed to explore species differences in diameter effects, and (3) did not affect qualitatively any results on species differences in survival. Among the five continuous exposure-variables, the strongest correlations appeared between the three forms of DIREX and FETCH (for all possible pairs: $r_s = 0.64–0.89$, $n = 3255$, $P <0.001$); their correlations with FETCHw were slightly weaker ($r_s = 0.47–0.59$, $n = 3255$, $P <0.001$). For the main analysis, we only selected the standard and most information-rich FETCH, though it still co-varied with the tree position (Kruskal-Wallis ANOVA: $P <0.001$). Yet, after constructing the final model, we tested the possible additional effects of the other exposure variables using Type I models.

To take into account the potential shade from other trees on the cut, we only used post-harvest density of the trees for simplicity, though the tree densities declined during the study period. This variable was independent of the other cut-level variable – site type (see Figure 2), and there was only one significant correlation with the cut-level average value of a tree-level variable: post-harvest densities were higher in case of smaller-diameter trees (r_s = -0.31, $n = 102$, $P =0.001$).

Table 2 Variables for the survival analysis of individual trees: division between levels, means, standard deviations and range

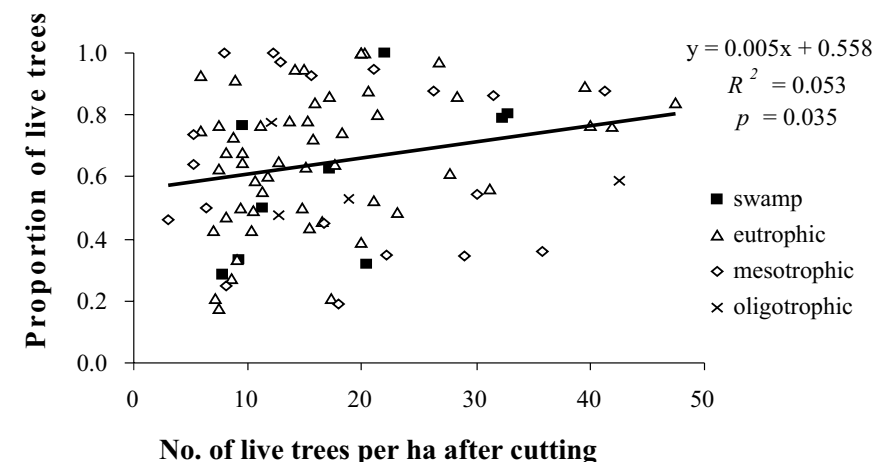| Variable (no. of groups)	Mean	S.D.	min.	max.
Level 1: Geographical location – 3 regions				
Level 2: Stand variables – 102 cuts				
Site type (4)				
Post-harvest density	15.9	10.1	2.3	47.5
Level 3: Tree variables – 3255 trees				
Tree position (5)				
FETCH	1047.4	430.1	130	2210
FETCHw	316.7	205.7	15	900
DIREX30	6.5	1.7	1	8
DIREX60	5.2	2.0	0	8
DIREX90	4.2	2.0	0	8
Diameter	30.2	11.2	14	100
Species (6)				

Fig. 2 The average retention-tree survival in relation to their post-harvest density in 85 cut areas (with at least 10 trees retained) during the study. For illustrative purposes, the cuts of different site types have been distinguished

Results

Mortality of Retention Trees

The average retention levels on the 102 cut sites were 15.9 (range 2–48) live trees per ha and 3.8 (range 0–22) standing dead trees per ha. The average volume of live retention trees was 15.6 (range 1.5-60.2) m³ ha⁻¹, which accounts for 6% of the average growing stock in mature stands in the Estonian state forests (Adermann 2004). Most trees had been retained solitarily.

The total number of live retention trees decreased 35% (from 2153 to 1405 trees) in six years in the cut areas of 2001, and 36% (from 1102 to 711 trees) in five years in the cut areas of 2002 (Figure 3A). The annual mortality rates were, on average, 6.8 ± 4.6% for the 2001 cut areas and 8.2 ± 6.2% for the 2002 cut areas, respectively, but these rates decreased during the study (Figure 3B). In preliminary general linear model explaining annual mortality via post-cut year and the cutting year ("cohort"), the latter was non-significant ($F_1 = 0.05$, $P = 0.83$). After pooling the data from the two cohorts, the univariate linear regression between % annual mortality (y) and post-cut year (x) was highly significant: $y = 13.15-1.79x$ (coefficient S.E. = 0.34; $n = 6$; $P = 0.006$).

The loss of total live-tree volume in the study period was higher than

of tree numbers: 42% (from 13.1 m³ to 7.6 m³ per ha) for the 2001 cut areas and 38% (from 14.1 m³ to 8.8 m³ per ha) for the 2002 cut areas. These losses provided 4.4 m³ of downed dead trunks and 1 m³ of standing dead trees ha⁻¹ from each „cohort". Compared with live tree volumes, the retained *Populus tremula* produced relatively large amounts of dead wood, especially snags (Figure 4).

Of the 1139 retention-tree deaths, 89.6% were wind damages (incl. 69.1% uprooting and 20.5% trunk breakage) and 10.4% died on foot. The dominant causes of death differed between tree species: uprooting was most frequent for *Tilia cordata* (100%) and *Pinus sylvestris* (84%), trunk breakage for *Alnus glutinosa* (60%), *Alnus incana* (50%) and *Populus tremula* (43%), and death on foot for *Fraxinus excelsior* (61%) (Table 1). There was no clear pattern in uprooting frequency along with the site type gradient: 28% of retained trees were windthrown in oligotrophic type (n =104), 31% in mesotrophic (n = 505), 21% in eutrophic (n = 2371) and 35% in swamp type (n = 275) during the study.

Projection of the annual tree survival rates indicated that, in case of natural mortality only, 29–38% of retained live trees are likely to be present after 40 years (closed mid-aged stand) and 22–29% in 100-year-old stands. If commercial thinning is added, these proportions will be 18–28% and 9–15%, respectively (Figure 5).
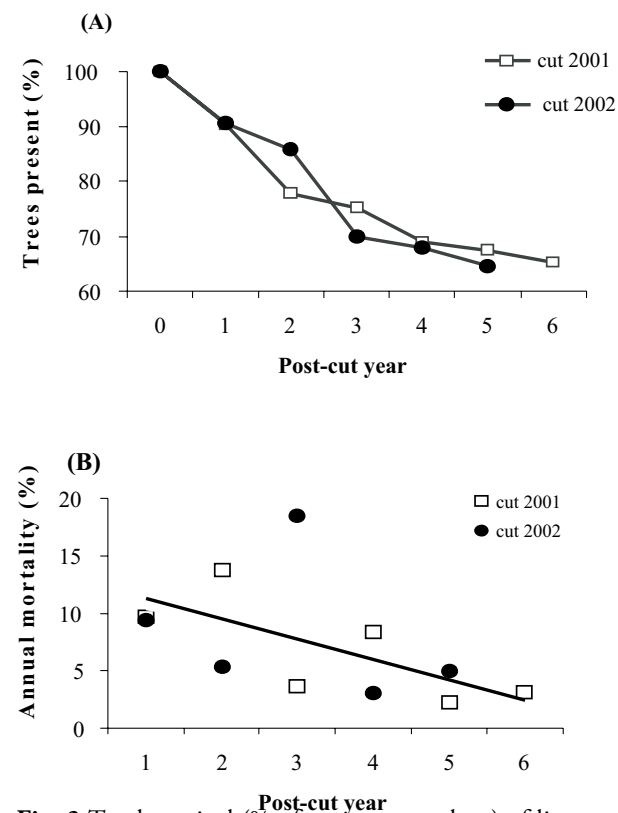

Fig. 3 Total survival (% of post-cut numbers) of live retention trees (A) and annual mortality (% of the numbers of the previous year; B) in the sites cut in 2001 (*n* = 2153 trees) and 2002 (*n* = 1102 trees)
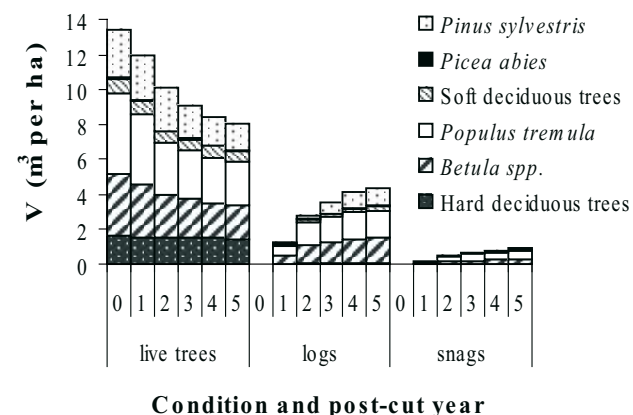

Fig. 4 Reduction of the total live-tree volumes and the resulting accumulation of coarse woody debris during five years
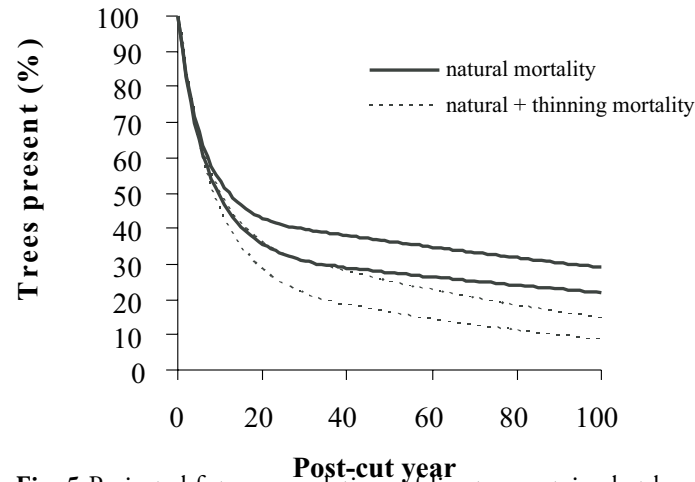
Fig. 5 Projected future populations of live trees retained at harvest (minimum and maximum scenarios for each mortality regime)

Determinants of tree mortality

Of the seven variables considered, geographical region and site type were omitted from the final model (Table 3) due to their non-significance ($P > 0.2$) in any multivariate combination (see Appendix for their descriptive statistics). Among tree species (see also Appendix), hard deciduous trees survived best (Tukey's tests for all post-hoc contrasts significant at $P < 0.001$), followed by soft deciduous trees ($P < 0.001$ for the contrasts with birch, aspen and pine; $P = 0.015$ for spruce). Diameter affected survival (Table 3) depending on tree species: positively in aspen (*coefficient* 0.022 ± 0.008 S.E.; $t_{3237} = 2.8$, $P = 0.006$) and in soft deciduous trees (*coefficient* 0.047 ± 0.018 S.E.; $t_{3237} = 2.7$, $P = 0.008$), and negatively in birch (*coefficient* -0.031 ± 0.010 S.E.; $t_{3237} = 3.0$, $P = 0.003$). Without the nesting approach (see Material and Methods), diameter seemed to have no effect ($F_{1, 3242} = 2.0$; $P = 0.16$)

The expected effects of all exposure variables were confirmed (Table 3): the initial retention density had a positive effect (see also Figure 2), FETCH had a negative effect (Figure 6A), the trees near forest edge survived much better than in the middle of the cuts (Tukey's test: $P < 0.001$) and, compared with the latter, pre-cut edges enhanced tree survival in the sequence: earlier cut edge ($P = 0.036$) < road edge ($P < 0.001$) < field edge ($P = 0.003$) (Figure 6B). However, among the pre-cut edges, only

the earlier cut-field edge contrast was marginally significant (Tukey's test: $P = 0.066$).

Using Type I tests to explore the effects of the four exposure variables, which were initially considered redundant to FETCH, indicated a significant additional contribution of FETCHw only ($F_{1, 3236} = 7.1$, $P = 0.008$). Moreover, when FETCHw was considered in the initial model instead of FETCH, the latter revealed no additional effect ($F_{1, 867} = 2.2$, $P = 0.14$). In a similar procedure, DIREX30, DIREX60 and DIREX90 all appeared to be significant predictors of tree survival ($P < 0.004$), but FETCH retained its additional contribution to each of them ($P < 0.05$).

Table 3 Fixed effects of the multivariate model for the 5–6-year survival of individual live retention trees

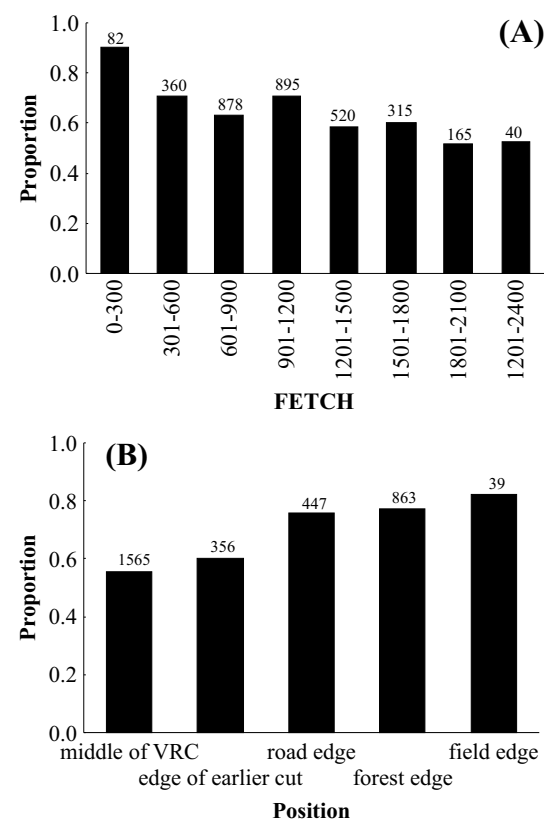| Variable	DF	*F*	*P*
Species	5; 3237	6.56	<0.0001
Diameter[a]	6; 3237	4.44	0.0002
Post-harvest density	1; 84.2	7.52	0.0074
Tree position	4; 3237	17.49	<0.0001
FETCH	1; 759.5	11.49	0.0007

[a]nested in species

Fig. 6 Tree survival during the study in relation to FETCH (A), and tree position (B). The numbers above the bars are sample sizes

Discussion

Our study confirmed that wind damage is the proximate cause for the majority (90%) of tree deaths on retention cuts. Hence, the survival factors extracted by our analyses should be mostly interpreted in the light of wind-resistance, and these may differ from the situations where other mortality agents contribute more. For example, wind-caused deaths formed only 77% in a study by Busby et al. (2006), and may even remain below 50% for certain tree species (e.g., *Alnus glutinosa* and *Fraxinus*; Wolf et al. 2004). Also in our study, hard deciduous trees relatively often died on foot. In particular, *Fraxinus excelsior* probably suffered from disease (probably a fungal pathogen; see Stenlid et al. 2005) since many individuals were dying also in adjacent forests (R.R., personal observations). However, it is also likely that other mortality agents contributed to the death of many wind-damaged trees; thus, wind-induced mortality cannot be unequivocally distinguished for a separate analysis. Despite these

unavoidable limitations, our results on the three key issues of retention-tree survival (pre-adaptations, spatial aspects, long-term prospects) lead to important practical implications as discussed below.

Pre-adaptations of the trees

In terms of pre-adaptations to post-cut conditions, our results suggested that tree species and tree location relative to pre-cut edge are the key variables to be considered in retention practices. Hard deciduous trees (mostly Fraxinus excelsior) survived best, followed by soft deciduous trees (mostly Tilia cordata and *Alnus glutinosa*) – a pattern roughly consistent with the hypothesis that shade-tolerant tree species are most wind-resistant (e.g., Canham et al. 2001; Peterson 2004). A well-known exception, having a below-average survival due to its shallower rooting (e.g., Peltola et al. 1999; Nicoll et al. 2006), was the only shade-tolerant coniferous species in our study area, *Picea abies*. Thus, VRC can increase the abundance of large individuals of shade-tolerant deciduous species that often disappear in even-aged forestry (e.g., Lõhmus et al. 2005). These species (most notably *Quercus robur*) also host distinct and species-rich biotic communities that are threatened in most clear-cutting forestry systems (e.g., Berg et al. 1994).

In previous case studies, windthrow probability has been found to increase (Canham et al. 2001; Peterson 2004) or decrease with tree diameter (Jull 2001; DeLong et al. 2001), yet in other cases medium-sized trees appear to be most susceptible (Lässig and Mocalov 2000; Beese 2001). Our results supported the view that, instead of a general relationship between tree diameter and survival, there are complicated species-dependent relationships (see Canham et al. 2001; Peterson 2004). As a preliminary approach, we thus encourage the retention of larger individuals of any given species (as required, for example, by the Swedish FSC-standard; The Swedich FSC-Council 1998) for their higher quality for threatened species (e.g., Lõhmus et al. 2006), but we call for species-specific studies to define conflicting cases in terms of tree survival. In Estonia, birch appeared to be the only species with a negative diameter-effect on survival, the reasons of which also deserve further study. At least, this species did not appear to be more close to maximum age limit than several others in our study (cf. Wolf et al. 2004).

We are not aware of previous field tests linking the survival of retention trees with their location relative to pre-cut edges, though unadapted trees are generally known to be more susceptible to wind – for example, if forests are opened up with clear-cutting or intensive thinning (e.g., Talkkari et al. 2000; Zeng et al. 2004; Lanquaye-Opoku and Mitchell 2005) or the trees have been retained solitarily rather than in clumps (Gibbons et al. 2007). Also, edge-trees have been reported to be less susceptible at old than fresh clear-cuts (Foster 1988; Zeng et al. 2004). Our analysis puts these findings into a general framework of individual adaptation and selective pre-cut mortality processes as illustrated by the decline of tree survival from the oldest (field) to medium-aged (road) and young pre-cut edges (previous cut area) and, finally, cut interior. A confounding factor may be that the wind-resistance near roads may have been improved by drainage ditches, which often run along the roads. Importantly, tree position remained highly significant even though the multivariate model considered actual exposure (FETCH) as well. Perhaps, the exposure variables describe mostly the selective mortality of trees, while the additional effect of tree-position accounts more for individual adaptation.

These results on pre-adaptation do not lead, however, to a straightforward recommendation to retain the trees growing near former forest edges – many threatened tree-dwelling species require the stable microclimate of forest interior conditions (Baldwin and Bradfield 2005; Gignac and Dale 2005), and may never be able to occupy the field- or road-edge trees. A reasonable compromise, then, could be to retain both (1) interior forest trees in case of small post-cut exposure (notably, near existing forest edge and at higher retention densities) for (re-)establishment by interior species, and (2) the pre-adapted trees in open conditions to provide habitats for disturbance-phase tree-dwelling species. Additional guidelines based on pre-adaptation are to prefer the dominant trees (Dunham and Cameron 2000; Jull and Sagar 2001) and to facilitate the adaptation process already in mid-aged stands by more extensive thinning around the future retention trees (Lohmander and Helles 1987).

Spatial aspects of tree retention

In agreement with many other (mostly univariate) analyses (e.g., Lohmander and Helles 1987; Ruel 2000; Beese 2001; Ruel et al. 2003; Walter and Maquire 2004; Scott and Mitchell 2005) the local spatial effects of surrounding forest and other retention trees appeared to be highly relevant for tree survival in our study – even though the retention levels were low, and decreasing in time. Previous studies have noticed a sharp increase in survival when retention levels exceed 20% (Scott and Mitchell 2005) and the survival may approach pre-cut values when over 50% of trees are retained (e.g., Conner et al. 1991; Coates 1997; Holgen et al. 2003). Regarding exposure, the novel aspects of our study emerged from the multivariate approach. First, after taking into account cardinal distances to forest edges (any type of FETCH or DIREX), location near forest edge retained an independent positive contribution to tree survival. Most probably, the survival increases sharply and non-linearly near forest edge – an aspect that is lost by simply summing the distances. Such a critical distance deserves further study, particularly in combination with the shade effects on sensitive tree-dwelling biota (for example, epiphytic lichens; Lõhmus et al. 2006). Second, a simpler, locally justified exposure variable – FETCHw – performed better than the standard FETCH, apparently because it considered dominating winds most important. Though sometimes storms from unusual directions may cause high tree-mortality (Ruel 2000; Ruel et al. 2001), this seemed to be not a general case in Estonia where wind-protection to retention trees from western sides of cut areas appears to be most important. To summarize, assessment of the shade provided by the surrounding post-cut forest edge (within 30 m) is a promising field technique for selecting retention trees, and regional modifications of general techniques may further enhance its efficacy.

In contrast to the local effects, we found no independent geographical and site-type differences. The former might be expected, for example, between areas differing in the frequency of severe storms that are strong determinants of overall tree mortality (e.g., Beese 2001; Ruel et al. 2001). To assess the importance of such random events, our study region may have been too small and/or the study period too short. In fact, the high 3rd post-cut year mortality in the cut areas of 2002 (Figure 3B), which were mostly situated in the Viljandi region, apparently resulted from a storm in January 2005. Untypically, the ground was frost-free and wet then, and Scots pines (concentrated to Viljandi region) suffered most. The absence of independent site-type effect has been previously reported by Achim et al. (2005) but it contrasts with the common understanding that the trees on wet or fertile soils are relatively wind-prone (Dunham and Cameron 2000; Ruel 2000; Mitchell et al. 2001; Vanha-Majamaa and Jalonen 2001). One additional reason in our study might have been the

drainage of wet cut-areas, which may have improved the wind-resistance of trees (Lohmander and Helles 1987). This may also explain why we did not find site type differences in the relative frequency of windthrow, which could be expected from the strong relationship between soil moisture and root-system structure (Lohmander and Helles 1987; Gardiner and Quine 2000; Scott and Mitchell 2005). In conclusion, our study did not reveal a necessity, in terms of tree survival, to differentiate tree-retention techniques geographically (at least within distances of a few hundred kilometres) or amongst site types but additional work on these aspects is needed.

The long-term prospects of green-tree retention

The recorded short-term mortality rates and their dynamics are in good accordance with the previous results. The 65% survival of retention trees in 5–6 post-cut years in hemiboreal Estonia is comparable with the 50–75% survival in similar time-frame in Canada (Beese 2001; Bradbury 2004; Scott and Mitchell 2005) and Oregon, USA (Busby et al. 2006). Also, the improvement of annual survival during post-cut years has previously been described for VRC (Beese 2001; Ruel et al. 2003; Busby et al. 2006) as well as for trees in riparian buffer strips (Ruel et al. 2001) and at clear-cut edges (Lohmander and Helles 1987; Mitchell et al. 2001). Therefore, given the absence of long-term monitoring results, our survival projections might be indicative for VRC planning also in other boreal or temperate areas.

To our knowledge, only Busby et al. (2006) have attempted to predict long-term survival of retention trees so far. Their result (14% survival after 100 years) was, however, based on two data points only and neither better survival prospects in forests nor cuttings were taken into account. Though it is unknown, when, and how exactly, the survival of retention trees might approach the levels typical to forests, our approach in general gave twice better 100-year survival estimates compared with Busby et al. (2006). Therefore, this process is highly relevant for future research. Similarly, while an accurate prediction of cuttings would be very complicated or even impossible, we showed that even routine thinnings might become a major mortality factor for the trees. In Estonia, many retained trees were actually seed trees, which traditionally are cut before canopy closure. Thus, without special protection, their long-term survival prospects and, thereby, efficacy for biodiversity protection will be much reduced.

More generally, the fact that most retention trees are likely to die before reaching the next forest generation indicates that their equally important function is the production of coarse debris.

The mortality aspects described above are particularly relevant given that even without human-induced mortality the projected densities of old retention trees in the next forest generation, and the coarse woody debris created by their death, would be much smaller than in natural forests. Hemiboreal old-growth forests normally contain 10–20 large (DBH>70) live trees per hectare (and many more having DBH >50 cm; Nilsson et al. 2002) and around 100 m^3/ha of coarse woody debris (Siitonen 2001), while the minima for threatened polypore fungi, for example, are 20 m^3/ha (Penttilä et al. 2004). In our study, the average initial abundance of retained live trees (a mere 16 trees or 16 m^3/ha) decreased by 30–40% during the 5–6 post-cut years already and was expected to decrease >70% in 100 years. Though the retention densities should be probably increased, the numerical targets of old-forests may be also inappropriate for managed forests. Therefore, the most urgent field of research is the minimum abundance of old live trees in the next forest generation, which might be derived, for example, from extinction thresholds of specific species inhabiting such trees. After setting the target, the current knowledge on long-term survival and its determinants could be used for developing sound guidelines for tree-retention levels and conditions.

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Appendix The average annual survival (S) of different tree species during the study according to the geographic area, site type, diameter class, and the position relative to edges. The survival estimates are shown for samples of at least 10 trees

	Populus tremula		*Betula* spp.		*Pinus sylvestris*		*Picea abies*		Soft deciduous trees[a]		Hard deciduous trees[b]	
	S	n	S	n	S	n	S	n	S	n	S	n
Geographic area												
Laeva	0.91	146	0.93	499	0.96	86	0.92	31	0.95	237	0.98	533
Alatskivi	0.88	183	0.82	243	0.87	25	0.88	10	0.95	86	0.98	103
Viljandi	0.96	132	0.93	286	0.91	536		6	0.93	71	1.00	42
Site type												
swamp		8	0.83	56	0.93	160		5	0.95	35	0.96	11
eutrophic	0.90	360	0.91	897	0.90	92	0.91	41	0.95	337	0.98	644
mesotrophic	0.95	80	0.92	72	0.91	307		1	0.96	22	0.97	23
oligotrophic	0.89	13		3	0.93	88						
Diameter												
<20 cm	0.83	22	0.95	118	0.95	22	0.92	16	0.94	168	0.98	294
21-30 cm	0.88	71	0.90	521	0.91	300	0.91	23	0.95	169	0.98	278
31-40 cm	0.93	108	0.90	302	0.91	261		6	0.95	45	0.99	71
41-50 cm	0.93	119	0.87	75	0.96	52			0.95	10	0.98	24
>51 cm	0.90	141	0.87	12	0.94	12		2		2	0.97	11
Position of trees												
Middle of VRC	0.89	231	0.89	562	0.89	308	0.81	15	0.92	157	0.98	291
Edge of earlier cut	0.88	56	0.88	107	0.92	58		2	0.95	56	0.99	71
Road edge	0.94	61	0.94	134	0.93	66		5	0.96	68	0.99	108
Field edge		8		9		6		1		4	1.00	11
Forest edge	0.95	105	0.94	216	0.95	209	0.94	24	0.97	109	0.99	197

[a] *Tilia cordata, Alnus glutinosa, A. incana* and *Salix caprea*
[b] *Fraxinus excelsior, Ulmus glabra, U. laevis, Quercus robur, Acer platanoides, Prunus padus* and *Sorbus aucuparia*

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LIST OF PUBLICATIONS

1.1. Publications indexed in the ISI Web of Science database:

Rosenvald, R., Lõhmus, A. 2007. For what, when and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management, published online Oct. 15, 2007. DOI: 10.1016/j.foreco.2007.09.016.

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