Journal of Forest Research

ISSN: 1341-6979 (Print) 1610-7403 (Online) Journal homepage: http://www.tandfonline.com/loi/tjfr20

Silviculture as a disturbance regime: the effects of clear-cutting, planting and thinning on polypore communities in mixed forests

Asko Lõhmus

To cite this article: Asko Lõhmus (2011) Silviculture as a disturbance regime: the effects of clear-cutting, planting and thinning on polypore communities in mixed forests, Journal of Forest Research, 16:3, 194-202, DOI: 10.1007/s10310-011-0256-7

To link to this article: https://doi.org/10.1007/s10310-011-0256-7

J For Res (2011) 16:194–202
DOI 10.1007/s10310-011-0256-7

SPECIAL FEATURE: ORIGINAL ARTICLE

Approaches for forest disturbances studies: natural variability and tree regeneration

Silviculture as a disturbance regime: the effects of clear-cutting, planting and thinning on polypore communities in mixed forests

Asko Lõhmus

Received: 1 May 2010 / Accepted: 14 January 2011 / Published online: 15 May 2011

Abstract The structure of modern forest landscapes is profoundly affected by human-caused disturbances, particularly forest management; however, the effects and prospects of individual silvicultural techniques are insufficiently understood. This study distinguishes the effects of clear-cutting, planting and thinning on species richness and community composition of polypore fungi. In 2008–2009, 181 forest compartments (ranging from naturally regenerated deciduous stands to planted *Picea abies* stands and 0–137 years post clear-cutting) were explored in a hemiboreal landscape subjected to even-aged management. Altogether 104 polypore species were recorded. For species richness, time since clear-cutting was the most influential factor at both stand and landscape scales, followed by thinning. Clear-cuts had distinct polypore communities (including several red-listed species) whose species richness declined in time. Following 20 years post clear-cutting, species richness started to increase along different community–composition pathways determined by regeneration type. The communities developed after planting were moderately species rich at stand scale but homogeneous over larger areas. Thus, at landscape scale, mature unmanaged naturally regenerated stands hosted most species; thinning reduced species richness by approximately 15%, and among thinned stands, planted areas had a further 9–22% fewer species than naturally regenerated areas. In such variably managed landscape, silviculture appeared to create particularly distinct communities in young stands on nutrient-rich soils, which naturally provide polypores with a rich supply of small deciduous snags absent from stands artificially planted with *P. abies* and intensively thinned.

Keywords Chronosequence · Disturbance-based silviculture · Fungi · Natural regeneration · Succession

Introduction

The compositional and functional heterogeneity of natural forests are largely created by various disturbances at different spatial and temporal scales (Sousa 1984; Kuuluvainen 2002). Because modern forest landscapes are increasingly disturbed by man, mostly for agriculture and timber production, there is concern over loss of heterogeneity in general and of biodiversity in particular (Lindenmayer 2009). Research is therefore needed on functional and compositional properties of ecosystems predominantly disturbed by commercial management (White and Jentsch 2001) and on the possibilities to improve management to better resemble natural processes (Kohm and Franklin 1997). While there is huge literature on forest species requirements and general comparisons of 'managed' and 'unmanaged' areas, the effects of different silvicultural measures on biodiversity have been insufficiently addressed (Jonsson et al. 2005; Lindenmayer 2009; Paillet et al. 2010; but see Rosenvald and Lõhmus 2008 for tree-retention effects).

This study explores how forestry operations affect communities of polypore fungi in even-aged forestry. Fungi in general are underrepresented in forest research,

---

Electronic supplementary material The online version of this article (doi:10.1007/s10310-011-0256-7) contains supplementary material, which is available to authorized users.

A. Lõhmus (✉)
Department of Zoology, Institute of Ecology and Earth Sciences,
University of Tartu, Vanemuise 46, 51014 Tartu, Estonia
e-mail: asko.lohmus@ut.ee

although they are very diverse and play a prominent role in ecosystem functioning (e.g. Lonsdale et al. 2008). Polypores comprise about 1200 species of basidiomycetes with distinct poroid fruit-bodies (Mueller et al. 2007); most of them are wood-inhabiting and some are mycorrhizal. Thus, polypores can be affected by disturbances that change the composition and dynamics of forest trees, and many species have become threatened by loss of their specific habitats in intensively managed forests (Niemelä 2005). Such disturbance dependency may be complex; for example, some parasitic polypores are able to kill trees themselves, while other species may require wood decayed by those particular or still other predecessor fungi (Niemelä et al. 1995; Stenlid et al. 2008). Importantly for field studies, fruit-bodies of many polypores are well detectable and thus suitable for exploring management impacts at stand scale (Berglund et al. 2005; Lõhmus 2009).

I use multivariate approaches to explicitly relate polypore community characteristics to three basic management techniques across a commercially managed landscape in Estonia, northern Europe: (1) clear-cutting, which produces chronosequences of even-aged stands; (2) artificial regeneration with a native conifer to replace natural regeneration of deciduous ‘pioneer’ species; and (3) thinning of young and mid-aged stands, and partial cutting and sanitary cutting (removal of dead and dying trees) in older stands. Previous chronosequence studies on polypores in dry boreal pine forests have demonstrated distinct communities in early-successional phase, and major effects of thinning and dead-tree removal later on (Sippola and Renvall 1999; Junninen et al. 2006). My study complements that research by exploring nutrient-rich mesic-to-wet lands further south where fires play a smaller role naturally and post-disturbance recovery is relatively rapid. I separate the effects of regeneration type, tree species diversity, timber-harvesting intensity and time. Considering previous work on wood-inhabiting fungi in closed-canopy stands (Bader et al. 1995; Heilmann-Clausen et al. 2005; Küffer and Senn-Irlet 2005), each of those expectably inter-correlated factors may affect polypore diversity, and may also lead to community differentiation according to the availability of natural versus man-made substrata (Müller et al. 2007).

The polypore community characteristics included are species richness, species composition and the number of red-listed species. Regarding community composition, I am most interested in the poorly known young stands, and the alternatives of natural versus artificial regeneration. Given the uniqueness of open early-successional and old-growth stages (Junninen et al. 2006), I ask whether some species are additionally confined to the stem-exclusion phase, which naturally contains much small-dimensioned deadwood because of the self-thinning processes.

Materials and methods

Study area

The study was carried out in eastern Estonia (58°15′N, 27°24′E) in a 4-km^2 forest landscape that was delineated using forest compartment borders and without prior knowledge on its fungal biota. Estonia is situated in the hemiboreal vegetation zone; mean air temperature is 17°C in July and −6.5°C in January; average precipitation is 600–700 mm year^{-1}.

Forest land (181 forest stands and cut areas) encompasses 94% of the study area, the rest being under small openings (roads, large ditches etc.), which were not explored. Typically of Estonian forests, the landscape is extensively drained and managed for timber using even-aged (clear-cutting based) systems, so that no natural streams or primaeval forests have been left but scattered old semi-natural stands of high conservation value still exist. All the stands originated from clear-cutting (no slash burning) and had been regenerated either naturally or planted in unscarified soil with Norway spruce (*Picea abies*), which seldom reaches upper canopy until the mature stage naturally. During the study, 19% of the forest land was clear-cut ≤20 years ago, 29% were young (21–40 years), 26% mid-aged (41–60 years) and 27% mature (61–100 years) stands. The area is managed by the Estonian State Forest Management Centre, certified according to the international Forest Stewardship Council scheme and ISO 14001 environmental management standard.

Three productive forest types dominate the area: typically naturally regenerated and deciduous-dominated stands of *Filipendula* (29% of forest land; mostly drained) and *Aegopodium* types (28%), and Norway spruce (*Picea abies*)-dominated or mixed stands of *Oxalis-Myrtillus* type (36%). The latter included most of the two artificial regeneration types—planted pure (≥80% of stand composition) spruce stands and initially planted stands that had developed into mixed stands (25–75% spruce)—practised in the area (15% and 12% of forest land, respectively). Most stands had one tree layer, but 16 mid-aged or mature stands were two-storeyed and 16 clear-cuts were not yet regenerated. The area hosts 11 commercially valued tree species, the most common in the upper storey being *P. abies* (on average, 41% of stand volume), *Betula* spp. (35%), *Alnus glutinosa* (13%), *Populus tremula* (6%) and *Fraxinus excelsior* (4%). Where present, the lower storey mostly comprised *P. abies*, *Tilia cordata* and *F. excelsior*. My field categorization of thinning and sanitary-cutting intensity based on stumps and slash in young-to-mature stands revealed that 24% (by area) had received no such treatment and 17% had a few stumps only, while 52% were conventionally managed (most slash left) and 7% were intensively managed (most slash removed). Figure 1 indicates the total areas by age and management category; Lõhmus (2011) presents a map of the study area.

Polypore survey and stand characterization

From September to November in 2008 and 2009, I surveyed each stand for fruit-bodies (sporocarps) of all polypore species. Survey time expenditure was adjusted first to stand area and then to substratum abundance (Fig. 2). The area-dependent time limits were set beforehand, and I carefully tried to avoid biased efforts towards 'better-looking' sites, such as older or better accessible stands. Based on my previous experience, I rapidly explored trunks and bases of live trees and deadwood items of all species, and repeatedly checked hand-samples of litter and moss in each stand, with the primary aim of finding most species and, secondarily, recording for each species the variety of its microhabitats (combinations of tree species, substratum type, decay stage and size category). For most species, one microhabitat type in one stand comprised one record, but rare and threatened species were also recorded at the accuracy of individual host trees. Dead fruit-bodies of perennial species were not considered. Most species were identified in the field, but difficult genera and species were collected and identified microscopically. The nomenclature follows Kotiranta et al. (2009).

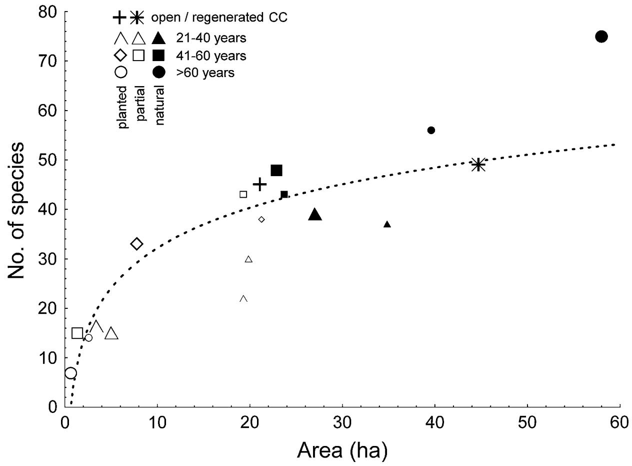

Fig. 1 Landscape-scale polypore richness in relation to the total area of stands of different management types (4 age classes, 3 regeneration types, 2 levels of thinning intensity). The *dashed line* represents a logarithmic relationship. *Large symbols* denote stands not thinned or having a few stumps only; *small symbols* are conventionally or intensively thinned stands. For clear-cuts (CC) only the incidence of regeneration is shown

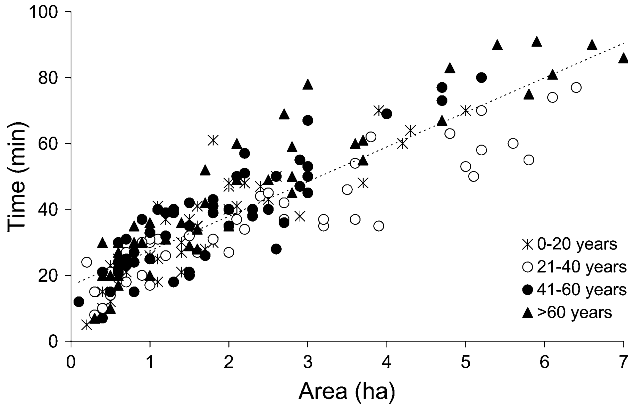

Fig. 2 Survey time in relation to stand area in four stand-age categories. $n = 181$ stands; linear function (*dashed line*) explains 78% of the total variation. Note the additional adjustment to substratum abundance, i.e. relatively shorter time expenditure in deadwood-poor young stands

Nine management-related environmental variables were estimated for each stand. Six variables were based on the database of the State Forest Management Service, but their estimates were critically evaluated in the field and a few minor corrections were made: (1) stand area (ha), (2) time since clear-cutting (TSC; years), (3) regeneration type (three categories; see above), (4) tree-species richness, (5) number of tree layers (0–2) and (6) proportion of Norway spruce in the stand. The estimates of tree-species richness are minima because, for technical reasons, only species reaching ≥5% relative abundance in tree layer were registered, and *Betula* spp. and *Salix* spp. were treated at the generic level. In case of clear-cuts with no tree layer established, tree-species richness and spruce abundance refer to the pre-cut stand, because polypores inhabited the legacies only. For two-storey stands, the proportion of spruce was estimated as a weighted average (the 1st layer having double weight compared with the 2nd layer). Three characteristics were estimated in the field with supporting data from the State Forest Service: (7) intensity of thinnings and sanitary cuttings (four categories; see above), (8) time since last cutting operation (years) and (9) number of European aspen (*Populus tremula*) trees (diameter at breast height ≥10 cm). Time since last cutting was roughly estimated according to the decay of slash, logs and stumps based on comparison with clear-cuts of known age, my previous experience, and literature. Since thinning residues become hardly detectable in about 20 years, I assigned a value of 25 years for all stands ≥25 years old having no visible residues. Aspen abundance was estimated for another study (Lõhmus 2011) but is included here given the significance of aspen for biodiversity.

There was expectably strong co-variation among several environmental variables. Notably, in 140 young-to-mature stands, higher thinning levels were accompanied with shorter time since the last cutting ($r_s = -0.79$, $P < 0.001$), and both of those management indicators were less pronounced in more naturally regenerated stands (for thinning intensity: $r_s = -0.26$, $P < 0.001$; for time since cutting: $r_s = 0.26$, $P < 0.001$). Moreover, since spruce abundance was related to regeneration type by definition and older stands were more often naturally regenerated ($r_s = 0.34$, $P < 0.001$), the proportion of spruce decreased ($r_s = -0.26$, $P = 0.002$) and tree-species richness increased ($r_s = 0.49$, $P < 0.001$) along stand age in the sample.

Data analyses

At the stand scale, I related the species richness of polypores to environmental variables using multifactor linear models (type III) where the survey time spent was included as a co-variate. Species richness of all polypores followed normal distribution and was analysed with general linear models (GLM); for the number of red-listed species (according to eBiodiversity 2010), generalized linear models (GLZ) based on Poisson distribution and log link were used. In GLZ, factor significance was estimated using likelihood-ratio tests; category contrasts for significant categorical factors were further explored using Wald statistic. Clear-cuts were modelled separately from forest stands because some factors (regeneration type, no. of tree layers) were less relevant and TSC had a distinct effect there (see “Results” section). The contribution of thinning intensity was separately checked against reduced models comprising only significant factors, and its four initial categories were pooled into two. That was necessary because thinning intensity was largely redundant with time since last cutting (see above), and several of its combinations with regeneration type were absent from the sample. Analyses were performed using STATISTICA 9.1 software.

I compared polypore communities among eight types of stands using non-metric multidimensional scaling (NMS) with Sørensen distance as the measure of dissimilarity using PC-ORD version 5.10. The stand types included clear-cuts; naturally regenerated young, mid-aged and mature stands, as well as young and mid-aged stands containing ≥80% and 25–75% planted Norway spruce. The data comprised presence/absence of each species found more than twice in the landscape (78 species). To reduce random deviations caused by the sparse distribution of polypores, small stands were omitted or pooled together (in case of adjacent stands of similar type and management history), so that the analysis included 52 stands of 3.5–7.7 ha size. NMS analyses were run for 1–4-dimensional solutions (90 runs with real and 100 runs with randomized data). Stress reduction was determined after 200 iterations using Monte Carlo tests. Final three-dimensional stress value was acceptable (16; $P < 0.01$). Quality of the data reduction and its distribution among the axes were calculated as coefficient of determination (r^2) between distances in the ordination space and distances in the original space. Differences in species composition between stand types were tested using multi-response permutation procedures (MRPP; McCune and Grace 2002). For interpreting gradients in the ordination space, five continuous environmental variables (nos. 2, 4, 6, 8 and 9 above) were included and their r^2 of the axes were calculated.

Results

Species richness

Altogether, 104 species of polypores were detected in the 181 stands. Of those, *Phellinus cinereus* and *P. nigricans* were both present (the former apparently more frequent), but they were treated collectively because of many specimens with intermediate characters. The three most common species (*Fomitopsis pinicola*, *Fomes fomentarius* and *Trichaptum abietinum*) occurred in more than 100 stands, while 16 species were found only in a single stand (see Electronic Supplementary Material).

At landscape scale, mature unmanaged naturally regenerated stands hosted most species both in absolute terms (75 species) and relative to area (Fig. 1). Residuals of the species–area relationship (Fig. 1; only those stand types covering ≥5 ha considered) indicated that conventionally or intensively thinned young and mature forests had, on average, 15% [±4%; 95% confidence interval (CI)] fewer species than stands of comparable age and regeneration type with no or a few stumps only. Only a few comparisons for regeneration type could be made, but among thinned stands, young planted stands had 22%

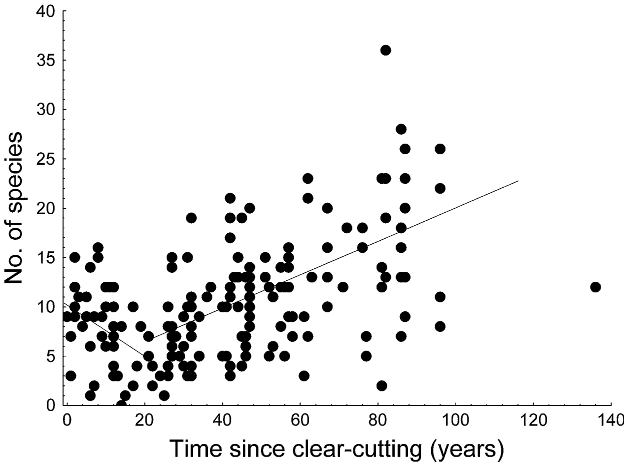

Fig. 3 The number of polypore species found in post clear-cutting chronosequence of 181 stands. The *regression lines* (separate for clear-cuts and forests) are for illustrative purposes only (see Table 1 for slopes in multifactor analyses)

Table 1 GLM for species richness of all polypores in clear-cut and forest stands

Factors	Age class and model statistics			
	Clear-cut (≤20 years)		Forests (>20 years)	
	Coefficient[a]	P	Coefficient[a]	P
Survey duration (min)	0.21 ± 0.03	<0.001	0.22 ± 0.02	<0.001
Time since clear-cutting (years)	−0.40 ± 0.10	<0.001	0.12 ± 0.01	<0.001
Time since cutting (years)	0.29 ± 0.14	0.047		0.198
No. of tree species		0.304		0.244
Picea abies (%)		0.975		0.332
Populus tremula (no. of trees)	−0.34 ± 0.10	0.007		0.474
No. of tree layers	n.a.	n.a.		0.137
Regeneration (3 types)	n.a.	n.a.		0.983
Intercept		0.340		0.616

[a] Coefficients (±SE) are shown for significant variables only

n.a. not applicable

fewer species than naturally regenerated ones, while that difference was 9% in the mid-aged stage, and there were no consistent differences between partly planted and naturally regenerated stands.

At stand scale, TSC was the most important factor for species richness, followed by thinning. TSC significantly interacted with stand-age category (GLM: $F_{3,172} = 2.7$, $P = 0.047$) when both were included in the model; such effect appeared because during the clear-cut phase species richness declined while it increased afterwards (Fig. 3; Table 1). In clear-cuts, polypore richness was lower in sites with more live aspens and shortly after the first thinning. In forests, no other factor contributed to TSC in the simple full model (Table 1), but a negative effect of thinning appeared after non-significant terms were removed from the model [GLZ, coefficient for moderate-to-intensive thinning = −0.63, standard error (SE) = 0.27, $P = 0.023$].

Species composition

NMS produced a 3-dimensional ordination space that described 86% of the variation in polypore community composition and included four patterns (Fig. 4):

1. Mature naturally regenerated stands had a central position in the ordination space. Coarse lying deadwood was the most frequent substratum in these stands, and polypores often grew on live trees (Table 2). Such stands had 14 rare species not found elsewhere and many frequent characteristic species (>50% records; see Electronic Supplementary Material), such as some parasites of old deciduous trees (*Inonotus obliquus*, *Phellinus alni*, *P. cinereus* and *P. tremulae*), follower-species of other polypores (*Gloeoporus dichrous* and *Pycnoporellus fulgens*) and species of lying deciduous deadwood (*Hyphodontia radula* and *Rigidoporus crocatus*). Compared with younger naturally regenerated stands, mature stands did not differ significantly from mid-aged forests (MRPP test: $P = 0.38$), but contrasts were evident between mature and young stands ($A = 0.19$; $P < 0.001$) and young and mid-aged stands ($A = 0.09$; $P = 0.026$);
2. Clear-cutting produced communities different from any other ($A = 0.13$ and $P = 0.027$ for partially planted young stands; $A = 0.19$–0.31 and $P < 0.01$ for other comparisons), separated by axis 1 related to TSC (Fig. 4a). Stumps became the most important substratum type (Table 2), and some whole polypore genera (*Antrodiella*, *Postia*, *Phellinus* and *Steccherinum*) almost disappeared. Characteristic species included *Trametes hirsuta*, *Lenzites betulinus* and *Funalia trogii* mostly on lying deadwood in open clear-cuts, *Gloeophyllum odoratum* and *Ganoderma lucidum* on decayed stumps and *Physisporinus sanguinolentus* and *Porotheleum fimbriatum* on decayed wood in regenerated sites;
3. Planting of spruce resulted in communities distinct from those in naturally regenerated young stands ($A = 0.14$–0.20; $P < 0.010$ for both pure and partial cultures), which were rich in deciduous tree species and received less thinning (axis 3). In the mid-aged stage, only pure planted stands still differed from those naturally regenerated ($A = 0.25$; $P = 0.016$). A characteristic of naturally regenerated stands was the importance of standing dead trees for polypores (Table 2), which was also the main substratum for *Daedaleopsis confragosa*—the only species mostly confined to young stands—and for *Dichomitus campestris* found in stands 37–47 years old. Landscape-scale benefits of planting for spruce-inhabiting species were minor: only *Skeletocutis carneogrisea* regularly occurred in planted, but not naturally regenerated, young stands; no such species were detected in mid-aged stands;

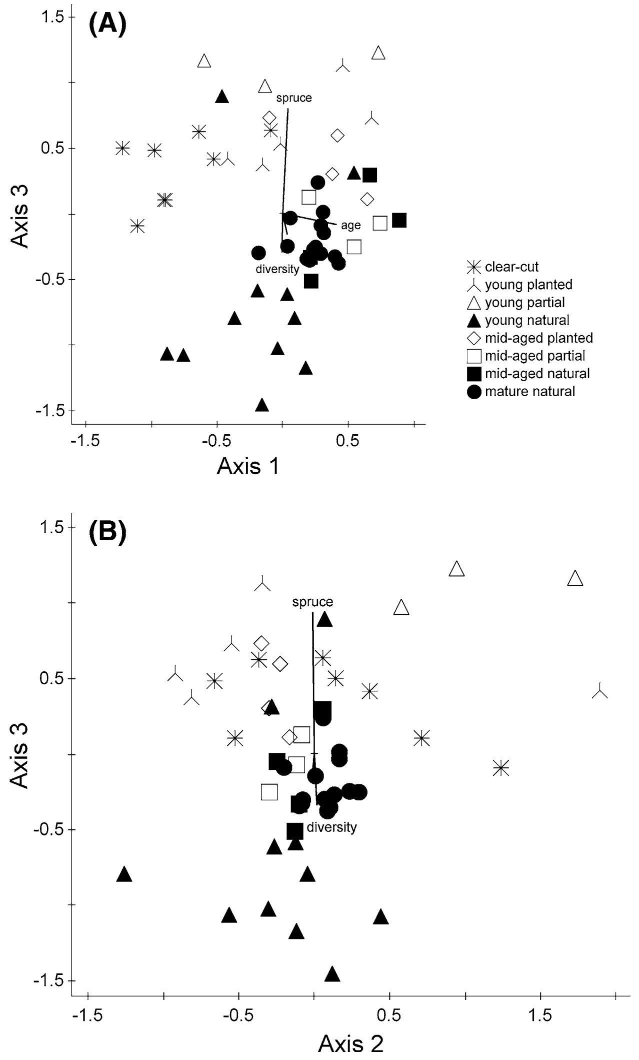

Fig. 4 Two-dimensional NMS-ordination plots of polypore communities in 52 stands of eight types. The three axes together describe 86% of variation in community composition (axis 1, 26%; axis 2, 32%; axis 3, 28%); environmental gradients are depicted as *lines* proportional in length to their co-variation with the axes (those with $r^2 \geq 0.2$ shown). ‘Natural’ refers to fully natural regeneration, ‘planted’ stands contain ≥80% and ‘partial’ stands 25–75% planted Norway spruce; stand age is categorized using 20-year intervals

4. Axis 2 was not related to any measured variable (Fig. 4b). It distinguished two types of young stands: semi-open areas, characteristically hosting *Gloeophyllum odoratum* and *Ganoderma* spp. on old cut stumps (high values), from thinned stands with species inhabiting fine woody debris (*Inonotus radiatus*, *Antrodiella serpula*) and logging slash (*Gloeophyllum sepiarium*).

Red-listed species

Altogether, 8 nationally red-listed species were recorded in 40 (22%) stands. Of those, *Ganoderma lucidum*, *Physisporinus sanguinolentus* and *Funalia trogii* were frequent in clear-cuts, and the two former species also inhabited planted spruce stands. Five other red-listed species were confined to naturally regenerated mature stands; of those *Rigidoporus crocatus* was frequent (notably on downed *Alnus glutinosa* trunks) and *Fomitopsis rosea*, *Phellinus nigrolimitatus*, *Protomerulius caryae* and *Steccherinum pseudozilingianum* were rare (see Electronic Supplementary Material).

Up to three red-listed species were found in a stand, depending on age category (GLZ: $\chi^2_3 = 26.9$, $P < 0.001$). Compared with mature stands, there were fewer such species in young (Wald’s test: $P = 0.042$) and mid-aged stands ($P = 0.036$) but more in clear-cuts ($P < 0.001$), where three species regularly occurred (see above). No other factor significantly contributed in clear-cuts. In forests, the result of the age-class analysis was mirrored as a positive effect of TSC (GLZ: $\chi^2_1 = 9.6$, $P = 0.002$); five other continuous variables were not significant. When added to the reduced model comprising survey time and TSC, incidence of moderate-to-intensive thinning was related to lower number of red-listed species ($\chi^2_1 = 4.7$, $P = 0.031$).

Discussion

In even-aged forestry, silvicultural treatments form complexes and follow spatial patterns determined by planning, land productivity, site accessibility and economic history. Therefore, at least in northern Europe, different treatments co-vary at scales ranging from individual stands (Kohv and Liira 2005) to their mosaics (Rosenvald and Lõhmus 2003) and whole regions (Angelstam et al. 2004). Consequently, their effects on biodiversity also co-occur and are difficult to separate, which has attracted researchers to integrate treatments into general ‘management intensity’ indices in field studies. However, my study clearly indicates that the effects are actually distinct and, by pooling them, crucial information for practical recommendations will be lost.

The main findings regarding clear-cutting were (1) a non-linear relationship between polypore species richness and time since harvesting, and (2) distinct and relatively species-rich early successional communities, which—similarly to those in boreal pine forests (Sippola and Renvall 1999; Junninen et al. 2006)—also hosted red-listed species. Of various factors that may account for the latter (see also Junninen et al. 2006) two merit attention here. First, cut stumps hosted taxa (*Ganoderma* species, *Gloeophyllum odoratum* and *Climacocystis borealis*), which in natural forests typically fruit on natural stumps and tip-up mounds of windthrown trees. Probably that effect was seen on axis 2 of community ordination. Those species may be

Table 2 Distribution (%) of polypore records among substrata in stands of different age and origin

Age (years)	Origin	Natural substrata[a]				Artificial substrata			*n*
		Live tree	Snag[b]	CWD[c]	FWD[c]	Stump	CWD[c]	FWD[c]	
≤20		9	6	15	6	37	10	16	592
21–40	Planted	3	12	25	23	11	9	19	102
	Partly planted	5	14	21	5	17	11	28	109
	Natural	8	38	15	19	7	4	8	322
41–60	Planted	2	13	22	20	11	12	19	365
	Partly planted	4	14	24	15	9	15	16	249
	Natural	12	26	24	21	5	5	7	500
>60	Planted	8	20	58	8	0	3	2	50
	Natural	19	18	40	14	3	4	2	1269
Total		12	18	28	15	11	7	9	3558

[a] Not shown: 34 records on tip-up mounds of windthrows

[b] Standing dead trees and natural stumps

[c] Lying deadwood: <10 cm (fine woody debris, FWD) or ≥10 cm in diameter (coarse woody debris, CWD)

vulnerable to extensive stump harvesting for biofuel in areas with few natural forests left. However, some of them apparently cause root- or butt-rot of live trees, so foresters may even find those declines desirable for timber production (Walmsley and Godbold 2010). Secondly, clear-cuts have deadwood of late-successional tree species (spruce, some broad-leaved trees) from the preceding mature stands in open conditions. Such deadwood is absent in the following young stands, which could explain the position of clear-cut communities on axis 3. It may also partly explain why the polypores considered characteristic of pine clear-cuts in Finland were non-pine species (see Junninen et al. 2006) that appeared widely distributed among stand ages in the mixed and planted stands of my study area.

The abundance of coarse woody debris is a major factor for the diversity of wood-inhabiting basidiomycetes (Stenlid et al. 2008), and it has similar U-shaped dynamics along clear-cutting chronosequence (Lõhmus et al. 2005; Ekbom et al. 2006) as I found for polypore richness. However, the post-harvesting decline of deadwood lasts until the mid-aged stage when half of large lying trunks may still be the legacies of previous stand in mixed hemiboreal forests (Lõhmus and Lõhmus 2005), while polypore richness reached its minimum much earlier (Fig. 3). Hence, the latter probably resulted from a complex of effects, such as passing the most favourable intermediate decay stages of coarse woody debris (see Ekbom et al. 2006 for a similar situation with bark microhabitat), loss of logging slash (probably contributing to diversity in clear-cuts; Junninen et al. 2006) and the appearance of new fine woody debris in young stands.

Polypore communities in young stands were the most variable, spanning across the whole ordination space and, despite similar stand-scale species richness, most clearly illustrating the divergence of community development and reduction of landscape-scale species richness caused by artificial planting. The effects of tree-species composition are expected given the host specificity of many polypores. However, there seemed to be also an interaction with stand age—the communities of partly planted stands converged through stand development (Fig. 4), which resembles observations on birds (Baguette et al. 1994) and bryophytes (Ross-Davis and Frego 2002) in similar landscape mosaics. Altogether, the variation in community composition explained by planting (axis 3) was as large as that of stand age (axis 1), and deadwood supply was the most likely proximate cause for both (planted spruce stands are structurally distinct from mixed stands; Lõhmus et al. 2005). Note that, although Norway spruce is a long-term native species in Estonia (Niinemets and Saarse 2009), its planting affected fungi rather similarly to where it is an exotic species (e.g. Küffer and Senn-Irlet 2005; Quine and Humphrey 2010).

The value of young naturally regenerated deciduous stands for fungi is insufficiently known (Nordén et al. 2004). However, at substratum level, both the distinction between coniferous versus deciduous wood and among small fractions of woody debris (Küffer et al. 2008) as well as the diversity of deciduous trees (Heilmann-Clausen et al. 2005; Küffer and Senn-Irlet 2005) are fundamental. The typical supply of small snags in such stands is an important foraging ground for woodpeckers (Lõhmus et al. 2010), which are known to disperse fungi (Farris et al. 2004), and deadwood produced by self-thinning may have distinct biota (Lindhe et al. 2004). Hence, young stands probably have not only distinct communities but also adapted species, such as *D. confragosa* and *D. campestris* in this study. Note that post-clear-cutting thickets lack the abundant supply of large lying trunks of early decay, which appear after wildfires (e.g. Brassard and Chen 2008) and host the greatest variety of wood-inhabiting organisms (Jonsson et al. 2005). Such impoverishment certainly contributed to the scarcity of polypores, including red-listed and specific species, in young stands (see Junninen et al. 2006 for such effect in pine forests). Studies on tree-retention practices should address whether that effect could be mitigated, but a result difficult to explain was the negative relationship between polypore species richness and abundance of aspen in clear-cut areas (cf. Junninen et al. 2007), and the lack of any effect of aspen in forests. Possibly, aspen-rich stands lacked some other important deciduous tree species or conditions.

Concurring with previous studies (Küffer and Senn-Irlet 2005; Junninen et al. 2006; Müller et al. 2007; Stenlid et al. 2008), thinning showed contrasting effects on polypore communities. First, it provided fungi in closed-canopy stands with new slash (negative values of axis 2) and cut stumps preferentially occupied, for example, by *Skeletocutis amorpha* and *Postia stiptica* (see Electronic Supplementary Material). Possibly, the positive effect of time since thinning in clear-cuts also referred to lagged colonization of slash by polypores. However, those effects were overridden by negative impacts at both stand and landscape scales, which probably included mostly removal of dying and dead trees and destruction of lying deadwood.

To summarize, even-aged silviculture creates habitats such as open early-successional and naturally regenerated young stands, which add to the well-known value of old forests for polypore fungi. However, those values may be lost through artificial planting of conifers and intensive thinning, and young planted spruce stands are apparently among the most distinct anthropogenic communities in hemiboreal forest landscapes. Hence, to sustain polypore richness at landscape scale, silvicultural disturbances should be well planned to leave sufficient areas for natural regeneration, retain variability in stands during thinnings and complement commercial landscapes with sufficiently large, protected old-growth forests.

Acknowledgments I thank Piret Lõhmus for help with PC-ORD. Kaisa Junninen and an anonymous referee constructively commented on the manuscript. The research was supported by the Estonian Science Foundation (grant 7402), the State Forest Management Centre, the Estonian Ministry of Education and Science (project SF0180012s09) and the European Union through the European Regional Development Fund (Centre of Excellence FIBIR).

References

Angelstam P, Boutin S, Schmiegelow F, Villard MA, Drapeau P, Host G, Innes J, Isachenko G, Kuuluvainen T, Mönkkönen M, Niemelä J, Niemi G, Roberge JM, Spence J, Stone D (2004) Targets for boreal forest biodiversity conservation—a rationale for macroecological research and adaptive management. Ecol Bull 51:487–509

Bader P, Jansson S, Jonsson BG (1995) Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol Conserv 72:355–362

Baguette M, Deceuninck B, Muller Y (1994) Effect of spruce afforestation on bird community dynamics in a native broad-leaved forest area. Acta Oecol 15:275–288

Berglund H, Edman M, Ericson L (2005) Temporal variation of wood-fungi diversity in boreal old-growth forests: implications for monitoring. Ecol Appl 15:970–982

Brassard BW, Chen HYH (2008) Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems 11:1078–1090

eBiodiversity (2010) Estonian Red List of threatened species. http://elurikkus.ut.ee/prmt.php?lang=eng (Accessed 26 April 2010)

Ekbom BL, Schroeder M, Larsson S (2006) Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. For Ecol Manag 221:2–12

Farris KL, Huss MJ, Zack S (2004) The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor 106:50–59

Heilmann-Clausen J, Aude E, Christensen M (2005) Cryptogam communities on decaying deciduous wood–does tree species diversity matter? Biodivers Conserv 14:2061–2078

Jonsson BG, Kruys N, Ranius T (2005) Ecology of species living on dead wood—lessons for dead wood management. Silva Fenn 39:289–309

Junninen K, Similä M, Kouki J, Kotiranta H (2006) Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29:75–83

Junninen K, Penttilä R, Martikainen P (2007) Fallen retention aspen trees on clear-cuts can be important habitats for red-listed polypores: a case study in Finland. Biodivers Conserv 16:475–490

Kohm KA, Franklin JF (eds) (1997) Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington

Kohv K, Liira J (2005) Anthropogenic effects on vegetation structure of the boreal forest in Estonia. Scand J Forest Res 20:122–134

Kotiranta H, Saarenoksa R, Kytövuori I (2009) Aphyllophoroid fungi of Finland. A check-list with ecology, distribution, and threat categories. Norrlinia 19:1–223

Küffer N, Senn-Irlet B (2005) Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests. Biodivers Conserv 14:2419–2435

Küffer N, Gillet F, Senn-Irlet B, Aragno M, Job D (2008) Ecological determinants of fungal diversity on dead wood in European forests. Fungal Divers 30:83–95

Kuuluvainen T (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn 36:97–125

Lindenmayer DB (2009) Forest wildlife management and conservation. Ann NY Acad Sci 1162:284–310

Lindhe A, Åsenblad N, Toresson HG (2004) Cut logs and high stumps of spruce, birch, aspen and oak—nine years of saproxylic fungi succession. Biol Conserv 119:443–454

Lõhmus A (2009) Factors of species-specific detectability in conservation assessments of poorly studied taxa: the case of polypore fungi. Biol Conserv 142:2792–2796

Lõhmus A (2011) Aspen-inhabiting Aphyllophoroid fungi in a managed forest landscape in Estonia. Scand J Forest Res (in press)

Lõhmus A, Lõhmus P (2005) Coarse woody debris in mid-aged stands: abandoned agricultural versus long-term forest land. Can J For Res 35:1502–1506

Lõhmus A, Lõhmus P, Remm J, Vellak K (2005) Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. For Ecol Manag 216:201–215

Lõhmus A, Kinks R, Soon M (2010) The importance of dead-wood supply for woodpeckers in Estonia. Balt For 16:71–86

Lonsdale D, Pautasso M, Holdenrieder O (2008) Wood-decaying fungi in the forest: conservation needs and management options. Eur J For Res 127:1–22

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

Mueller GM, Schmit JP, Leacock PR, Buyck B, Cifuentes J, Desjardin DE, Halling RE, Hjortstam K, Iturriaga T, Larsson KH, Lodge DJ, May TW, Minter D, Rajchenberg M, Redhead SA, Ryvarden L, Trappe JM, Watling R, Wu Q (2007) Global diversity and distribution of macrofungi. Biodivers Conserv 16:37–48

Müller J, Engel H, Blaschke M (2007) Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. Eur J For Res 126:513–527

Niemelä T (2005) Polypores—lignicolous fungi. Norrlinia 13:1–320 (in Finnish with English summary)

Niemelä T, Renvall P, Penttilä R (1995) Interactions of fungi at late stages of wood decomposition. Ann Bot Fenn 32:141–152

Niinemets E, Saarse L (2009) Holocene vegetation and land-use dynamics of south-eastern Estonia. Quatern Int 207:104–116

Nordén B, Götmark F, Tönnberg M, Ryberg M (2004) Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. For Ecol Manag 194:235–248

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma RJ, De Bruyn L, Fuhr M, Grandin U, Kanka R, Lundin L, Lugue S, Magura T, Matesanz S, Mészáros I, Sebastià MT, Schmidt W, Standovár T, Tóthmérész B, Uotila A, Valladares F, Vellak K, Virtanen R (2010) Does biodiversity differ between managed and unmanaged forests? A meta-analysis on species richness in Europe. Conserv Biol 24:101–112

Quine CP, Humphrey JW (2010) Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? Biodivers Conserv 19:1503–1512

Rosenvald R, Lõhmus A (2003) Nesting of the black stork (*Ciconia nigra*) and white-tailed eagle (*Haliaeetus albicilla*) in relation to forest management. For Ecol Manag 185:217–223

Rosenvald R, Lõhmus A (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. For Ecol Manag 255:1–15

Ross-Davis AL, Frego KA (2002) Comparison of plantations and naturally regenerated clearcuts in the Acadian Forest: forest floor bryophyte community and habitat features. Can J Bot 80:21–33

Sippola AL, Renvall P (1999) Wood-decomposing fungi and seed-tree cutting: a 40 year perspective. For Ecol Manag 115:183–201

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Stenlid J, Penttilä R, Dahlberg A (2008) Wood-decay basidiomycetes in boreal forests: distribution and community development. In: Boddy L, Frankland JC, van West P (eds) Ecology of saprotrophic basidiomycetes. Elsevier Academic, Boston, pp 239–262

Walmsley JD, Godbold DL (2010) Stump harvesting for bioenergy—a review of the environmental impacts. Forestry 83:17–38

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399–450. Springer, Berlin