The effect of buffer strip width and selective logging on streamside polypore communities

Authors

Maiju Peura[1,2], Anna Oldén[1,2], Merja Elo[1,2], Janne Kotiaho[1,2], Mikko Mönkkönen[1,2], Panu Halme[1,2]

Affiliations

[1] Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

[2] School of Resource Wisdom, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Emails

maiju.peura@jyu.fi, anna.m.olden@jyu.fi, merja.elo@jyu.fi, janne.kotiaho@jyu.fi, mikko.monkkonen@jyu.fi, panu.halme@jyu.fi

Correspoding author

Maiju Peura; Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland; +358440332588; maiju.peura@jyu.fi

Abstract

Preserving streamside forest habitats or buffer strips is considered to reduce forestry related biodiversity loss in commercial forest landscapes. However, it is still unclear what type of management in and near streamside forests can be undertaken without compromising their biodiversity and its natural change through succession. We tested the before-after-control impacts of forested buffer strips (15 or 30 m wide, with or without selective logging) preserved after clear-cutting, on the changes of polypore communities in streamside boreal forests in Finland. Manipulations in 28 sites produced four treatment classes, the community compositions of which were compared with 7 unmanaged controls before and 12 years after the manipulations. The polypore community composition in 15 m wide buffer strips changed differently than that in controls, and resembled the community composition typically found in production forests. Moreover, selective logging tended to homogenize polypore communities. These responses of polypore communities indicate that the natural biodiversity and succession of streamside forests was disturbed in both 15 m wide and selectively logged buffer strips. Streamside forests in non-logged 30 m wide buffer strips seemed to retain the natural polypore community composition and succession, at least during the 12 years period.

Key words: buffer zone, dead wood, key habitat, partial harvesting, riparian forest

1 Introduction

Most of the boreal forests are under timber production, which has decreased their biodiversity values by homogenizing forest structures and species compositions (Esseen et al. 1997; Kuuluvainen and Gauthier 2018). Preserving small-scaled forest patches, which provide valuable habitat for specialized and red-listed species, is considered to reduce forestry related biodiversity loss in forest landscapes (Ericsson et al. 2005; Timonen et al. 2010, 2011). These assumed biodiversity-hotspots are called woodland key habitats and they are protected by law or forest certification in most Fennoscandian countries (Timonen et al. 2010). However, it is still unclear what type of management, if any, can be allowed in and near these habitats without disturbing their biodiversity in the long term (Marczak et al. 2010; Timonen et al. 2010, 2011; Hylander and Weibull 2012; Kuglerová et al. 2014). Streamside forests represent one of the most common key habitat types in Fennoscandia (Timonen et al. 2010; Selonen and Kotiaho 2013) and their retention is a part of sustainable forest management internationally (e.g., Lee et al. 2004; Sweeney and Newbold 2014).

Most commercial boreal forests are still managed under rotation forestry with clear-cuts (Kuuluvainen and Gauthier 2018), while streamside forests are retained by leaving a forested buffer strip between the stream and the clear-cut area (Timonen et al. 2010; Kuglerová et al. 2014). The width of the strip varies but they can be narrow (from few meters to tens of meters) (Lee et al. 2004; Selonen and Kotiaho 2013) and prone to strong edge effects (Murcia 1995), which extend at least 20-50 m into the forest from the edge (Aune et al. 2005; Ylisirniö et al. 2016). Edges are exposed to disturbances and they are usually warmer and drier than inland forests (Murcia 1995). Moreover, many common generalist species in boreal forests favor edges and outcompete specialized species that require closed forest structures (Ruete et al. 2016). Therefore, the area of natural streamside habitat, which is not under the edge effect, can be very small or non-existent (Aune et al. 2005).

Previous studies in streamside habitats have suggested that the width of the buffer strips should be at least 30 to 45 m to preserve the natural microclimatic conditions and community composition of the streamside habitat biodiversity (Selonen and Kotiaho 2013; Sweeney and Newbold 2014; Oldén et al. 2019a, 2019b).

The forests in the immediate surroundings of streams have a special microclimate and forest structure that provide habitats for a diverse range of species (Naiman and Décamps 1997). The amount and diversity of dead wood, which is a critical resource for many forest-dwelling species, can be higher in streamside habitats than in other production forests (Siitonen et al. 2009; Sweeney and Newbold 2014). In Fennoscandia, the average amount of dead wood in managed forests is 5 m^3 ha^{-1} or below, whereas for many dead wood dependent species the critical threshold may be around 20 m^3ha^{-1} (Junninen and Komonen 2011). Siitonen et al. (2009) reported that the average volume of dead wood in streamside habitats in southern Finland was 11.7 m^3 ha^{-1} and that only 15% of streamside forests fulfilled the threshold of 20 m^3 ha^{-1}.

Dead wood dependent polypores are pathogens of living trees and decomposers of dead trees and therefore crucial for forest ecosystems' natural functioning and succession (Junninen and Komonen 2011; Stokland et al. 2012). In addition, as polypores are sensitive to changes in substrate quality and abiotic conditions, they are widely used as biological indicators in ecological research (Halme et al. 2017). Findings about the importance of streamside forests in supporting polypore communities are controversial (Junninen and Kouki 2006; Hottola and Siitonen 2008). Streamside habitats can support polypore species richness but their function in the conservation of threatened polypores is uncertain. In general, key habitats, such as streamside forests, are often too small in size and isolated to preserve viable populations of specialized and rare species, especially if surrounded by clear-cuts (Sippola et al. 2005; Ylisirniö et al. 2016). Several studies have reported that the composition of polypore communities changes near forest edges (Snäll and Jonsson 2001; Siitonen et al. 2005; Ruete et al. 2016).

Streamside forests are often productive and thus interesting from the economic point of view (Lundström et al. 2018). Therefore, leaving wide buffer strips next to clear-cuts can evoke significant costs. The Finnish Forest Act (*Forest act* 2013) allows selective logging in the streamside key habitats, provided their characteristic features, i.e. natural forest structure, microclimatic conditions and growing conditions, are not altered. If selective logging can be performed without altering these characteristic features, it could be a way to decrease the costs of retaining wider buffer strips. Relative to clear-cutting, selective logging can reduce forestry related biodiversity loss (Joelsson et al. 2017; Vanha-Majamaa et al. 2017; Oldén et al. 2019a), but it nevertheless is likely to disturb microclimatic conditions and species composition relative to unmanaged old-growth forests (Bader et al. 1995; Sippola et al. 2001; Oldén et al. 2019b). However, the impacts of selective logging on the changes of species community composition are still poorly understood.

The aim of this study was to determine the impact of forested buffer strip width and the impact of selective logging of the buffer strips on the formation of dead wood and on the succession of polypore species community composition in streamside habitats in Finnish boreal forests. The streamside habitat was assumed to be the forested area from 0 to 15 m from the stream, which is included in the buffer strips. The width of the buffer strip between a stream and a clear-cut area (15 or 30 m) and selective logging within it were manipulated forming four buffer strip treatments, which were compared with unmanaged controls 12 years after treatment loggings. Study forests were 80–100 years old mature forests and expected to slowly change towards natural old-growth forest structure and species composition. Therefore, natural changes were likely to occur also in the control sites and our aim was to determine whether the treatments disturb the natural succession. We tested for differences in changes over time in the formation of dead wood, the number of polypore species and individuals, the polypore community composition, and the homogenization of the polypore communities among sites, between treatments and in relation to controls.

2 Materials and methods

2.1 Study design

Our 35 study sites, representing spruce (*Picea abies*) dominated and mature streamside forests, were located in production forest landscapes in southern and middle boreal region (Oldén et al. 2019a). There was only one study site along each stream. All of the sites were classified as Forest Act Habitats meaning that streamside forests were in a natural or nearly natural state. Before the treatment manipulations, the minimum distance to the nearest clear-cut area was 80 m, sites had not been managed during recent decades and the dominant trees were 80-100 years old. Thus, forests were expected to slowly develop towards old-growth conditions. In treatment manipulations, 7 sites were left as unmanaged control sites and loggings were conducted in 28 sites during the winter 2005-2006. As part of the logging operations, the adjacent upland forest on one side of the stream was clear-cut and one of four buffer strip treatments was applied between the stream and the clear-cut area: 30 m wide buffer strip without selective logging (5 sites), 30 m wide buffer strip with selective logging (8 sites), 15 m wide buffer strip without selective logging (6 sites) or 15 m wide buffer strip with selective logging (9 sites) (Fig. 1a). In selective loggings, 30% of the basal area of the forested buffer strip was evenly logged from the whole buffer strip width. The logged trees were mainly the largest trees. More information on study design and sites is found in Oldén et al. (2019a, 2019b).

2.2 Data collection

Dead wood and polypores were inventoried in late September – early November 2004 before the treatments and the inventory was repeated in late September – early November 2017, i.e. 12 growing seasons after the treatments. Dead wood was measured from 0.045 ha study plots and polypores from 0.1 ha plots (Fig. 1b). In this study, the immediate surrounding of a stream (from 0 to 15 m from a stream) was considered to be the actual streamside key habitat. Therefore in treatments with a 15 m wide buffer strip, the clear-cut was immediately next to study area whereas in treatments with a 30 m wide buffer strip, there was a 15 m wide strip (from 15 to 30 m from a stream) between the study area and the clear-cut (Fig. 1a). We did not have the dead wood data from 5 sites (one control site, two 30 m wide buffer strip sites with selective logging, and one 15 m wide buffer strip site with and one without selective logging), so the number of sites with dead wood data was 30.

Dead trees and their fragments with a diameter ≥ 5 cm and length ≥ 1.3 m were inventoried (thus excluding stumps). For each trunk and a fragment of a trunk, the length, diameter, tree species and decay stage was recorded. For the whole trunks, the diameter at 1.3 m height was measured, and for the fragments of the trunks the diameter at the middle of the fragment. The decay stages 1–5 were classified as follows (Renvall 1995): (1) hard, a knife penetrates by pushing only a few mm into the wood; (2) relatively hard, knife penetrates 1–2 cm in depth; (3) relatively soft, knife penetrates 3–5 cm in depth, (4) soft throughout, (5) very soft, can be moulded by hand. Volumes of whole dead trees were calculated based on the volume formulas of spruce (*Picae abies*), pine (*Pinus sylvestris*) and birch (*Betula pendula* and *pubescens*), the latter of which was applied for all deciduous tree species (Laasasenaho and Snellman 1983). Volumes of dead tree fragments were calculated using the formula of a cylinder.

Polypores were surveyed by observing their fruiting bodies from the dead and living trees with length ≥ 1.3 m and diameter ≥ 5 cm at 1.3 m height. Several fruiting bodies of the same species in one dead or living tree trunk or fragment of a trunk were considered as one individual. Only living fruiting bodies of perennial species were recorded but both living and dead fruiting bodies of annual species were recorded. If species identification in the field was not possible, a specimen was collected and identified under a microscope. The nomenclature and division of species follows Niemelä (2016) but *Phellinus igniarius coll.* included species *P. igniarius*, *P. alni* and *P. cinereus*, and *Postia leucomallellla coll.* included *species P. calvenda and P.rufsecens*. We classified red-listed species according to Kotiranta et al. (2019).

Treatment loggings have caused changes in abiotic microclimatic conditions (Oldén et al. 2019b) and can disturb biotic conditions through altered dead wood dynamics (Mäenpää et al. unpublished). Early colonizers can produce fruiting bodies soon after the colonization and on the other hand, the fruiting success of existing species can be disturbed due to changed abiotic conditions (Jönsson et al. 2008; Moore et al. 2008). Therefore, the early impacts of altered abiotic and biotic conditions on polypore community succession can be detected after 12 years.

2.3 Statistical analyses

2.3.1 Dead wood and numbers of polypore species and individuals

Most polypore species are specialized with regards to the tree species, size, mortality factor and decay stage of the trees (Junninen and Komonen 2011; Stokland et al. 2012). However in this study, our aim was not to deeply explore the dead wood profile and its impacts on polypore communities, and thus we only divided the resources between fresh (decay stages 1,2) and old dead wood (decay stages 3,4,5). We calculated the change in the volume of fresh and old dead wood between 2004 and 2017 separately for each site. The change of fresh decaying wood indicates the change in the formation of new dead wood, which is the one that can mainly be altered due to buffer strip treatments during the 12 years.

Similarly, we calculated the changes in the number of polypore species and the number of individuals for each site by subtracting the numbers observed in 2004 from those observed in 2017. These changes were calculated for all species as a group, in addition to which they were calculated separately for red-listed species as a group.

The calculated changes were not normally distributed so to test if there were differences in the changes among treatments we conducted non-parametric Anova, Kruskall-Wallis tests by ranks (function *kurskal.test* in R-package stats). To further test if the changes in buffer strip treatments differed from the control treatment we conducted Dunn's multiple comparison tests by ranks (function *dunn.test* in R-package dunn.test)

2.3.2 Polypore communities

To estimate the differences in polypore communities among sites and years we calculated and tested for differences in their semi-metric abundance-based (i.e., taking the number of individuals into account) Bray-Curtis dissimilarity measures (function *vegdist* in R-package Vegan). This dissimilarity measure is widely used and shown to be good in detecting ecological gradients. The measure varies between 0 and 1, with 1 meaning total dissimilarity between communities (no shared species). In addition, we repeated the analyses applying precence-absence based Sørensen measure. Polypore fruiting bodies were not detected at all from three sites before the treatment manipulations (one control site, one 30 m wide buffer strip site with selective logging and one 15 m wide buffer strip without selective logging), so we removed these sites from the community-level analyses. Due to this one polypore species (*Heterobasidion parviporum*) was not included in the community-level analyses as it was detected only in one site in 2017 and this site did not have fruiting bodies in 2004.

First, we analysed the impacts of buffer treatments on the mean community composition. We compared separately the mean community composition of each buffer treatment with the composition of control before and after the treatment manipulations using a permutational Manova, Permanova (function *adonis2* in R-package Vegan, a multivariate analog of analysis of variance). Explanatory factors were the four treatment contrasts: each buffer strip treatment compared with the control treatment. To test if the treatments change polypore communities differently compared with controls we ran a Permanova where we used the interactions of each treatment contrast and year as explanatory variables. We used study site as a strata to constrain permutations within sites. To directly test the effect of selective logging and to compare the effects of different buffer strip widths on the change of polypore community composition, we also analyzed data without the controls. In these analyzes, explanatory factors were the width of the buffer strip (15 m or 30 m), selective logging (yes or no), year and their interactions.

Second, we studied the impacts of buffer treatments on the dispersion in community composition. Decreased dispersion in community composition indicates homogenization, i.e. sites become more similar to each other in community composition. We compared the dispersion of each buffer treatment with the dispersion of control before and after the treatment manipulations using the analysis of multivariate homogeneity of group dispersions (*betadisper* in R-package Vegan, a multivariate analogue of Levene's test for homogeneity of variances) and permutations (*permutest.betadisper* in R-package Vegan). To test if buffer treatments changed the dispersion of communities differently than controls, we first used *betadisper* to extract the distance of each site to the centroid of the sites of the same treatment and year. *Betadisper* does not allow using more than one explanatory variable in the analysis, so we extracted the distances and used Anova (with Type II sums of squares) to test for the effects of the interaction between each treatment contrast and year (*Anova* in R-package car). As in the Permanova-analyses above, we also analyzed the data without controls to test for the effects of buffer strip width and selective logging among the buffer strip sites.

We also illustrated these community changes in different treatments with ordination using non-metric multidimensional scaling (NMDS, function *metaMDS* in R-package Vegan). Moreover, we tested if there were species associated with specific treatments before and after the treatment manipulations using multi-level pattern analysis (function *multipatt* in R-package Indicspecies).

The results of all community analyses above are reported with Bray-Curtis dissimilarity measures in the main text, but the results of the same analyses with Sørensen dissimilarity are fully reported in the Supplementary material. In all permutation tests, significances were tested using a randomization test with 9999 permutations. All statistical analyses were performed using R version 3.5.1 (R Development Core Team 2014). The references for the R-packages are available in Table S1.

3 Results

3.1 Dead wood

The formation of fresh dead wood (decay stages 1,2) tended to increase during the study period in all treatments (Figure 2a). The average volume of fresh dead wood was on average (± SD) 5.4 ± 5.6 $m^3\ ha^{-1}$ in 2004 and 20.0 ± 22.2 $m^3\ ha^{-1}$ in 2017. However, compared with controls, the formation of fresh dead wood increased less in 30 m wide buffer strips with selective logging (Dunn's test: Z_{df}=$-2.62_{1,12}$, p=0.044). The volume of old dead wood (decay stages 3,4,5) tended to remain at similar levels in 2004 and 2017 in all treatments (Figure 2b). The average volume (± SD) of old dead wood (decay stages 3,4,5) was 9.9 ± 21.4 m^3 ha^{-1} in 2004 and 6.7 ± 8.0 m^3 ha^{-1} in 2017. There were no significant differences among treatments in the change of old dead wood volume (Kruskal-Wallis: Chi-square$_{df}$=2.10$_{4, 27}$, p=0.718).

3.2 Numbers of polypore species and individuals

In total 62 different polypore species were recorded, of which 41 species were found in 2004 and 50 in 2017 (Table S2). The total number of individuals had doubled during the study period, as it was 320 in 2004 and 656 in 2017. The number of species per site (Fig. 2c) and the number of individuals per site (Fig. 2d) tended to increase in all treatments. The site-level number of species increased similarly among all treatments (Kruskal-Wallis: Chi-square$_{df}$=4.71$_{4,32}$, p=0.320). However, compared with controls, the site-level number of polypore individuals increased more in 15 m wide buffer strips with selective logging (Dunn's test: Z_{df}=-2.62$_{1,16}$, p= 0.009).

One red list species was observed in 2004, and seven in 2017, of which five different species were found in controls, two in 30 m wide strips without selective logging, two in 30 m wide strips with selective logging and two in 15 m wide strips with selective logging (Table S2). There were many sites without red-listed species and variation among sites was high so there were no significant differences among treatments in the change of site-level number of red-listed species (Kruskal-Wallis: Chi-squared$_{df}$ = 5.13$_{4,32}$, p = 0.280) or individuals (Kruskal-Wallis: Chi-squared$_{df}$ = 4.63$_{4,32}$, p = 0.330).

3.3 Polypore communities

3.3.1 Community composition

The mean community composition was similar to controls in all buffer strip treatments before the manipulations in 2004 (Table 1a, Fig. 3a). In contrast, the mean community composition was similar to controls only in non-logged 30 m wide buffer strips after the manipulations in 2017, and differed from the controls in both types of 15 m wide buffer strips and in 30 m wide buffer strips with selective logging (Table 1a, Fig. 3a).

The community composition of polypores had changed between years 2004 and 2017 in all sites (Fig. 3b). However, communities in both types of 15 m wide buffer strips showed changes that deviated from the changes in controls (Fig. 3). In controls, the changes tended to be inconsistent in direction whereas in 15 m wide buffer strips, changes tended to be more directional and towards species not found in the controls. (Fig. 3b). However, mean changes in community composition differed significantly from the controls only in 15 m wide buffer strips with selective logging (Table 2a). In non-logged 15 m wide buffer strips, the directions of change in community composition were less consistent (Fig. 3b) and the number of sites within the treatment was the smallest so the deviation from the control was not captured by Permanova. The mean community composition in selectively logged 30 m wide buffer strips changed roughly to the same direction as the composition in controls (Fig. 3b), and therefore these changes were not statistically different, although the compositions themselves differed in 2017 (Table 1a, Fig. 3a). Moreover, communities in 15 m and 30 m wide buffer strips changed differently but selective logging did not affect the change in mean community composition at either buffer strip width (Table 3a).

3.3.2 Community dispersion

The dispersion in community composition among sites was similar to controls in all treatments before the treatment manipulations in 2004 (Table 1b, Fig. 3a). After the manipulations in 2017, the dispersion in community composition was still similar to the controls in all treatments with the exception of the 15 m wide buffer strips with selective logging where the dispersion was smaller (Table 1b, Fig. 3a). Despite this, the dispersion in community composition changed differently than in controls in 15 m wide buffers without selective logging (Table 2b), where the dispersion seemed to be slightly increased compared to other treatments (Fig. 3a). The dispersion in community composition decreased in both buffer treatments with selective logging (Table 3b, Fig. 3a). However, the change of dispersion in buffer strip treatments with selective logging did not differ significantly from the change of dispersion in controls as it seemed to decrease slightly as well. Nevertheless, when the sites with different buffer strips were compared, selective logging caused a decrease in dispersion, while buffer strip width did not impact the change in dispersion (Table 3b).

3.3.3 Species associated with treatments

Except for one species (*Phellinus punctatus*) that was associated with controls, there were no species associated with treatments prior to treatment manipulations (Table S3). After the manipulations in 2017, there were three species (*Gloeophyllum sepiarium*, *Antrodia serialis* and *Postia tephroleuca*), which were associated with both types of 15 m wide buffer strips (Table S3). In addition, *Postia caesia* was associated with all buffer strip treatments, except the non-logged 30 m wide buffer strips (Table S2). These associated polypore species are mostly generalist species and typically found in production forests (Niemelä 2016). The direction of change of community composition in both types of 15 m wide buffer strips tended to be towards these species (Fig. 3). In addition, even though not significantly associated with the 15 m wide buffers, the abundance of two generalist species (*Fomitopsi*s *pinicola* and *Trichaptum abietinum*) increased in 15 m wide buffer strips after treatment manipulations (Table S2). Moreover, in 2017 three species (*Phellinus tremulae*, *Postia ptychogaster* and *Trichaptum fuscoviolaceum*) were associated with 15 m wide buffer stirps without selective logging and one species (*Antrodiella pallescens*) was associated with 30 m wide buffer strips withouth selective logging (Table S3).

3.3.4 Species presence vs. abundance

Communities were similar in buffer strip treatments and controls before the treatment manipulations in 2004 also when species presence-absence (Sørensen dissimilarity) was only considered (Table S4). After the manipulations in 2017, fewer buffer strip treatment differed from the control when species presence-absence was only considered than when abundance (Bray-Curtis dissimilarity) was considered. In 2017, only 15 m wide buffer strips differed from the controls in the mean community composition and 15 m wide buffer strips with selective logging in the dispersion of community composition (Table S4). The changes in mean composition and dispersion did not differ between any logging treatment and the control (Table S5). Similarly, the width of the buffer strip or selective logging did not affect the changes in mean composition and dispersion (Table S6). Therefore, the largest effects of management on communities were captured via increased abundance of certain species, such as species associated with specific treatments in 2017 (Table S3).

4 Discussion

4.1 The width of the buffer strips

Species richness and number of individuals tended to increase in all treatments 12 years after the manipulations. However, the community composition in 15 m wide buffer strips changed differently than that in controls and 30 m wide buffer strips, and after the manipulations, resembled the composition typically found in production forests. These results were not surprising, as narrow buffer strips are prone to strong edge effects, which has been identified in these sites also as increased abundance of windthrows (Mäenpää et al. unpublished) and as altered microclimatic conditions (Oldén et al. 2019b). In this study, we did not separate the impacts of substrate availability and abiotic conditions on polypores but the occurrence and increased abundances of certain species in narrow buffer strips indicate that polypore communities were disturbed through changes in both of them. *G. sepiarium* favours open and warm habitats (Snäll and Jonsson 2001;

Siitonen et al. 2005) provided by these narrow strips (Oldén et al. 2019b). *F. pinicola, T. abietinum, T. fuscoviolaceum* and *A. serialis* colonize recently felled dead trees in early and intermediate decay stages (Jönsson et al. 2008; Niemelä 2016), which were common in our narrow buffer strips due to the high number of windthrows (Mäenpää et al. unpublished). Moreover, two *Postia* species, which are common also in production forests (Niemelä 2016), were abundant in 15 m wide buffer strips. These responses of polypore species community support earlier conclusions the natural species composition of streamside habitats is disturbed in narrow buffer strips (Selonen and Kotiaho 2013; Sweeney and Newbold 2014; Oldén et al. 2019a, 2019b).

The natural like succession of streamside polypore communities appeared not to be disturbed if the width of the forested buffer strip between the stream and the clear-cut was 30 m wide and not selectively logged. In this case, the outer half of the buffer strip (from 15 to 30 m from the stream) seemed to protect the streamside habitat (from 0 to 15 m from the stream) from the strongest edge effect. However, an edge effect often travels deeper than 15 m into the forest (Murcia 1995; Ylisirniö et al. 2016) and the moisture conditions were found to be altered also in 30 m wide buffer strips in these study sites (Oldén et al. 2019b). Polypore communities are sensitive to these changes in microclimate even if their substrate availability is not disturbed (Moore et al. 2008). Moreover, negative responses of species can be slow due to extinction debt and thus may not yet be visible after 12 years (Junninen and Komonen 2011; Hylander and Weibull 2012). Therefore, based on our study it is too early to conclude that 30 m wide buffer strips would be wide enough to preserve the natural biodiversity of streamside habitats in the long term.

To retain biodiversity in streamside habitats, several studies have suggested that the width of buffer strip between a stream and a clear-cut area should be more than 30 m, depending on the features of the site and its surrounding landscape (Wenger 1999; Kuglerová et al. 2014; Sweeney and Newbold

2014; Oldén et al. 2019b). We did not explore other environmental factors in this study but, for example, the structure of the surrounding forest (Oldén et al. 2019b), topography (Wenger 1999; Sweeney and Newbold 2014) and the width of the moist habitat area (Kuglerová et al. 2014) can influence the needed width of the buffer strip to protect the biodiversity of streamside habitats.

4.2 Selective logging

Selective logging seemed to cause the homogenization of polypore communities when compared to buffer strips that had not been selectively logged. Such decreased variation in communities among sites with selective logging indicates that selective logging disturbed the natural variation in polypore communities, which is typically high in natural forests (Abrego et al. 2014). Moreover, compared with unmanaged controls, the formation of fresh dead wood was smaller in 30 m wide buffer strips with selective logging. This indicates that the continuity and diversity of dead wood resources in the future can be disturbed. These negative impacts of selective logging were not surprising either as previous studies in boreal forests have reported that selective logging can reduce the availability of dead wood resources and the richness of polypore species even decades after loggings (Bader et al. 1995; Sippola et al. 2001).

In narrow buffer strips with selective logging, the edge effect is strong and the direct impact of selective logging is probably smaller than the impact of the edge. In wider buffer strips with selective logging, the selective logging can affect the streamside habitat in two ways: directly by changing the forest structure in the streamside key habitat (from 0 to 15 m from the stream in this study) and indirectly by increasing the edge effect through the selectively logged outer half of the buffer (from 15 to 30 m from the stream). In any case, based on this and previous research in streamside forests, selective logging should not be applied, at least in the actual key habitat, if the aim is to retain the natural biodiversity and its succession (Lundström et al. 2018; Oldén et al. 2019b).

However, if selective logging is applied in surrounding forests beyond the 30 m instead of clear-cutting, this could reduce the negative effects of the adjacent loggings on streamside habitats (Braithwaite and Mallik 2012). In this case, the non-logged buffer strip between the stream and the production forest stand could be potentially narrower than 30 m. Despite the increased interest towards the possibilities of continuous cover forestry, such as selective logging, to reduce forestry related biodiversity loss in boreal commercial forests (Joelsson et al. 2017; Vanha-Majamaa et al. 2017), the strength of edge effect between an ecologically valuable habitat and a forest managed with continuous cover forestry has not been measured. However, continuous cover forestry affects microclimate less than clear-cuts at the stand scale (Zheng et al. 2000) and continuous cover forestry applied at the landscape scale can reduce the occurrence of windthrows (Pukkala et al. 2016). Therefore, the edge effect of continuous cover forestry is likely less severe than the effect of clear-cuts. This alternative forestry method has been suggested to be economically profitable (Tahvonen et al. 2010). Hence, managing forest stands next to a streamside habitat under continuous cover forestry could be beneficial from both economic and ecological perspectives. Future studies should explore more the possibilities of alternative forestry methods in the surrounding landscape to reduce negative edge effects on streamside habitats.

4.3 Key habitats and buffer strips as conservation tools

In general, the function of small retained forest patches, such as key habitats or buffer strips, as a conservation tool has been questioned, especially, from the perspective of red-listed species (Marczak et al. 2010; Timonen et al. 2011). Hottola et al. (2008) found that the number of red-listed polypore species was not significantly larger in streamside habitats than in spruce-dominated mature production forests in the same regions. However, some of their study sites were younger than in our study, all streamside habitats did not fulfill the criteria of key habitats defined by the Finnish Forest Act, and the forest management in and near streamside habitats was not controlled. In our study, only one red-listed species was found in 2004 when the volume of dead wood was small in many sites. However, in 2017 many sites fulfilled the threshold of 20 m^3 ha^{-1} dead wood (Junninen and Komonen 2011) and seven different red-listed species were found, whereof five species were found in the control sites. Thus, our study suggests that streamside key habitats, at least those defined by the Finnish Forest Act, and when allowed to develop through natural succession, can provide important habitats for red-listed polypores in forest landscapes. However, their long-term capacity to support the populations of sensitive species is not known (Junninen and Komonen 2011; Timonen et al. 2011).

Previous research suggests that while different types of key habitats or retained buffer strips can provide habitats for dead wood dependent species (Jönsson and Jonsson 2007; Siitonen et al. 2009; Hylander and Weibull 2012; Sverdrup-Thygeson et al. 2014), they may be too isolated and small in size to preserve viable populations of sensitive and specialized species in the long term (Junninen and Kouki 2006; Hottola and Siitonen 2008; Junninen and Komonen 2011; Ylisirniö et al. 2016). On the other hand, retained habitat patches or buffer strips themselves can support existing conservation networks by increasing the habitat connectivity at least for species with moderate dispersal ability (Laita et al. 2010). Nevertheless, in the case of streamside habitats, fragmentation may not be as problematic as, for example, in the case of old-growth forest patches, since streams form connected networks of habitats if forested buffer strips are wide enough and retained continuously. However, to guarantee the effectiveness of limited conservation efforts in commercial forest landscapes, small-scale efforts, such as retention trees in neighboring stands (Gustafsson et al. 2012) and less intensive forestry methods could be allocated to the vicinity of key habitats or buffer strips to protect them more from the negative impacts of forest management in the surrounding landscape.

4.4 Conclusions

We studied the management of streamside habitats in boreal Fennoscandia by manipulating the width of the forested buffer strip and selective logging within the buffer strips. The responses in polypore communities and dead wood formation 12 years after the manipulations showed that the natural biodiversity and its succession was disturbed in 15 m wide buffer strips and in selectively logged buffer strips. The disturbance was mainly detected in the changed species composition and not in terms of overall species diversity. Streamside habitats in non-logged 30 m wide buffer strips seemed to retain the natural like polypore community composition and its succession. However, based on previous studies, it is too early to conclude that 30 m wide strips would be wide enough to safeguard the preservation of natural biodiversity in streamside habitats in the long term. Therefore, large-scale spatial planning, which takes into account the adjacent forests next to streamside habitats, is needed to secure their effectiveness in conservation.

Acknowledgement We are grateful to Ville Selonen and Tuomas Talvitie for collecting the pre-manipulation data, and to Miia Kokkonen, Hennariikka Mäenpää and Suvi Järvenpää for their assistance in collecting the post-manipulation data. Moreover, we thank Jonna Timonen and Katriina Peltonen for their advice on collecting the data. This study was funded by Finnish Ministry of Agriculture and Forestry, Olvi Foundation (to M.P.) and Jenny and Antti Wihuri Foundation (to M.P.).

References

Abrego, N., García-Baquero, G., Halme, P., Ovaskainen, O., and Salcedo, I. 2014. Community turnover of wood-inhabiting fungi across hierarchical spatial scales. PLoS One **9**(7). doi:10.1371/journal.pone.0103416.

Aune, K., Jonsson, B.G., and Moen, J. 2005. Isolation and edge effects among woodland key habitats in Sweden: Is forest policy promoting fragmentation? Biol. Conserv. **124**(1): 89–95. doi:10.1016/j.biocon.2005.01.015.

Bader, P., Jansson, S., and Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. **72**(3): 355–362. doi:10.1016/0006-3207(94)00029-P.

Braithwaite, N.T., and Mallik, A.U. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. J. Appl. Ecol. **49**(1): 192–201. doi:10.1111/j.1365-2664.2011.02076.x.

Ericsson, T.S., Berglund, H., and Östlund, L. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biol. Conserv. **122**(2): 289–303. doi:10.1016/j.biocon.2004.07.019.

Esseen, P.-A., Ehnström, B., Ericson, L., and Sjöberg, K. 1997. Boreal Forests. Ecol. Bull. **46**: 16–47.

Forest act. 2013. Metsälaki 10 § (20.12.2013/1085)—Forest Act 10 § (20.12.2013/1085). Finlex. https://www.finlex.fi/en/laki/kaannokset/1996/en19961093.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., and Franklin, J.F. 2012. Retention Forestry to Maintain Multifunctional Forests: A World Perspective. Bioscience **62**(7): 633–645. doi:DOI 10.1525/bio.2012.62.7.6.

Halme, P., Holec, J., and Heilmann-Clausen, J. 2017. The history and future of fungi as biodiversity surrogates in forests. Fungal Ecol. **27**:193–201 doi:10.1016/j.funeco.2016.10.005.

Hottola, J., and Siitonen, J. 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodivers. Conserv. **17**:2559–2577. doi:10.1007/s10531-008-9317-4.

Hylander, K., and Weibull, H. 2012. Do time-lagged extinctions and colonizations change the interpretation of buffer strip effectiveness? - a study of riparian bryophytes in the first decade after logging. J. Appl. Ecol. **49**(6): 1316–1324. doi:10.1111/j.1365-2664.2012.02218.x.

Joelsson, K., Hjältén, J., Work, T., Gibb, H., Roberge, J.-M., and Löfroth, T. 2017. Uneven-aged silviculture can reduce negative effects of forest management on beetles. For. Ecol. Manage. **391**: 436–445. Elsevier B.V. doi:10.1016/j.foreco.2017.02.006.

Jönsson, M.T., Edman, M., and Jonsson, B.G. 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth Picea abies forest. J. Ecol. **96**(5): 1065–1075. doi:10.1111/j.1365-2745.2008.01411.x.

Jönsson, M.T., and Jonsson, B.G. 2007. Assessing coarse woody debris in Swedish woodland key habitats: Implications for conservation and management. For. Ecol. Manage. **242**(2–3): 363–373. doi:10.1016/j.foreco.2007.01.054.

Junninen, K., and Komonen, A. 2011. Conservation ecology of boreal polypores: A review. Biol. Conserv. **144**(1): 11–20. doi:10.1016/j.biocon.2010.07.010.

Junninen, K., and Kouki, J. 2006. Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? Scand. J. For. Res. **21**(1): 32–40. doi:10.1080/02827580500530009.

Kotiranta, H., Junninen, K., Halme, P., Kytövuori, I., von Bonsdorff, T., Niskanen, T., and Liimatainen, K. 2019. Aphyllophoroid fungi. *In* The 2019 Red List of Finnish Species. *Edited by* E. Hyvärinen, A. Juslén, E. Kemppainen, A. Uddström, and U.-M. Liukko. Ministry of the Environment & Finnish Environment Institute, Helsinki. pp. 234–248.

Kuglerová, L., Ågren, A., Jansson, R., and Laudon, H. 2014. Towards optimizing riparian buffer zones: Ecological and biogeochemical implications for forest management. For. Ecol. Manage. **334**: 74–84. doi:10.1016/j.foreco.2014.08.033.

Kuuluvainen, T., and Gauthier, S. 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. For. Ecosyst. **5**, 26. https://doi.org/10.1186/s40663-018-0142-2.

Laasasenaho, J., and Snellman, C.-G. 1983. Männyn, kuusen ja koivun tilavuustaulukot [in Finnish]. http://urn.fi/URN:ISBN:951-40-0999-1.

Laita, A., Mönkkönen, M., and Kotiaho, J.S. 2010. Woodland key habitats evaluated as part of a functional reserve network. Biol. Conserv. **143**(5): 1212–1227. doi:10.1016/j.biocon.2010.02.029.

Lee, P., Smyth, C., and Boutin, S. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. J. Environ. Manage. **70**(2): 165–180. doi:10.1016/j.jenvman.2003.11.009.

Lundström, J., Öhman, K., and Laudon, H. 2018. Comparing buffer zone alternatives in forest planning using a decision support system. Scand. J. For. Res. **33**(5): 493–501. doi:10.1080/02827581.2018.1441900.

Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L.R., and Richardson, J.S. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecol. Appl. **20**(1): 126–134. doi:10.1890/08-2064.1.

Moore, D., Gange, A.C., Cange, E.G., and Boddy, L. 2008. Fruit bodies: Their production and development in relation to environment. *In* Ecology of saprotrophic basidiomycetes. *Edited by* L. Boddy, J.C. Frankland, and P. van West. Elsevier Ltd. pp. 79–103.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. **10**(2): 58–62. doi:10.1016/S0169-5347(00)88977-6.

Naiman, R.J., and Décamps, H. 1997. The Ecology of Interfaces: Riparian Zones. Annu. Rev. Ecol.

Syst. **28**(1): 621–658. Annual Reviews. doi:10.1146/annurev.ecolsys.28.1.621.

Niemelä, T. 2016. Suomen käävät [in Finnish]. *Edited By* T. Niemelä. Finnish Museum of Natural History LUOMUS.

Oldén, A., Selonen, V.A.O., Lehkonen, E., and Kotiaho, J.S. 2019a. The effect of buffer strip width and selective logging on streamside plant communities. BMC Ecol. **19**,9. doi:10.1186/s12898-019-0225-0.

Oldén, A., Peura, M., Saine, S., Kotiaho, J.S., and Halme, P. 2019b. The effect of buffer strip width and selective logging on riparian forest microclimate. For. Ecol. Manage. **453**. doi:10.1016/j.foreco.2019.117623.

Pukkala, T., Laiho, O., and Lähde, E. 2016. Continuous cover management reduces wind damage. For. Ecol. Manage. **372**: 120–127. Elsevier B.V. doi:10.1016/j.foreco.2016.04.014.

R Development Core Team. 2014. R: A Language and Environment for Statistical Computing.

Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia **35**(1): 1–51. doi:10.29203/ka.1995.309.

Ruete, A., Snäll, T., and Jönsson, M. 2016. Dynamic anthropogenic edge effects on the distribution and diversity of fungi in fragmented old-growth forests. Ecol. Appl. **26**(5): 1475–1485. doi:10.1890/15-1271.

Selonen, V.A.O., and Kotiaho, J.S. 2013. Buffer strips can pre-empt extinction debt in boreal streamside habitats. BMC Ecol. **13**,24. doi:10.1186/1472-6785-13-24.

Siitonen, J., Hottola, J., and Immonen, A. 2009. Differences in stand characteristics between brook-Side key habitats and managed forests in southern finland. Silva Fenn. **43**(1):21–37. doi:Artn 21610.14214/Sf.216.

Siitonen, P., Lehtinen, A., and Siitonen, M. 2005. Effects of Forest Edges on the Distribution, Abundance, and Regional Persistence of Wood-Rotting Fungi. Conserv. Biol. **19**(1): 250–260.

doi:10.1111/j.1523-1739.2005.00232.x.

Sippola, A.-L., Lehesvirta, T., and Pertti, R. 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. Ecol. Bull. **49**: 243–254. Available from https://www.jstor.org/stable/20113280?seq=1#page_scan_tab_contents.

Sippola, A.L., Mönkkönen, M., and Renvall, P. 2005. Polypore diversity in the herb-rich woodland key habitats of Koli National Park in eastern Finland. Biol. Conserv. **126**(2): 260–269. doi:10.1016/j.biocon.2005.06.002.

Snäll, T., and Jonsson, B.G. 2001. Edge Effects on Six Polyporous Fungi Used as Old-Growth Indicators in Swedish Boreal Forest. Ecol. Bull. **49**: 255–262. Available from http://www.jstor.org/stable/20113281.

Stokland, J.N., Siitonen, J., and Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge University Press.

Sverdrup-Thygeson, A., Bendiksen, E., Birkemoe, T., and Larsson, K.H. 2014. Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. For. Ecol. Manage. **330**: 8–16. doi:10.1016/j.foreco.2014.06.036.

Sweeney, B.W., and Newbold, J.D. 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: A literature review. J. Am. Water Resour. Assoc. **50**(3):560–584. doi:10.1111/jawr.12203.

Tahvonen, O., Pukkala, T., Laiho, O., Lähde, E., and Niinimäki, S. 2010. Optimal management of uneven-aged Norway spruce stands. For. Ecol. Manage. **260**(1): 106–115. doi:10.1016/j.foreco.2010.04.006.

Timonen, J., Gustafsson, L., Kotiaho, J.S., and Mönkkönen, M. 2011. Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests. Biol. Conserv. **144**(8): 2061–2067. Elsevier Ltd. doi:10.1016/j.biocon.2011.02.016.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A., and

M̈nkk̈nen, M. 2010. Woodland key habitats in northern Europe: Concepts, inventory and protection. Scand. J. For. Res. **25**(4): 309–324. doi:10.1080/02827581.2010.497160.

Vanha-Majamaa, I., Shorohova, E., Kushnevskaya, H., and Jalonen, J. 2017. Resilience of understory vegetation after variable retention felling in boreal Norway spruce forests – A ten-year perspective. For. Ecol. Manage. **393**: 12–28. doi:10.1016/j.foreco.2017.02.040.

Wenger, S. 1999. A review of the scientific literature on riparian buffer width, extent and vegetation. Review for the Institute of Ecology, University of Georgia, Athens, USA. doi:30602-2202.

Ylisirniö, A.L., Mönkkönen, M., Hallikainen, V., Ranta-Maunus, T., and Kouki, J. 2016. Woodland key habitats in preserving polypore diversity in boreal forests: Effects of patch size, Stand structure and microclimate. For. Ecol. Manage. **373**:138–148. doi:10.1016/j.foreco.2016.04.042.

Zheng, D., Chen, J., Song, B., Xu, M., Sneed, P., and Jensen, R. 2000. Effects of silvicultural treatments on summer forestmicroclimate in southeastern Missouri Ozarks. Clim. Res. **15**: 45–69.

Tables

Table 1 Each buffer strip treatment compared with control separately in 2004 and in 2017 with Bray-Curtis dissimilarity in a) mean community composition (Permanova) and in b) dispersion in community composition (Betadisper).

	a) Community composition		b) Dispersion	
Explanatory factor	Pseudo-F_{df}	p	F_{df}	p
2004				
30m vs Control	$0.70_{1,31}$	0.763	$0.14_{1,31}$	0.717
30mSL vs Control	$0.85_{1,31}$	0.621	$0.52_{1,31}$	0.487
15m vs Control	$1.14_{1,31}$	0.302	$0.21_{1,31}$	0.656
15mSL vs Control	$0.59_{1,31}$	0.880	$0.01_{1,31}$	0.934
2017				
30m vs Control	$0.80_{1,31}$	0.628	$0.17_{1,31}$	0.693
30mSL vs Control	**$2.20_{1,31}$**	**0.017**	$0.23_{1,31}$	0.639
15m vs Control	**$2.81_{1,31}$**	**0.004**	$0.83_{1,31}$	0.387
15mSL vs Control	**$3.31_{1,31}$**	**0.003**	**$5.03_{1,31}$**	**0.043**

Statistically significant effects ($p < 0.05$) are indicated in bold.

Table 2 The effects of year, each buffer strip treatment compared with control, and their interactions with Bray-Curtis dissimilarity in a) mean community composition (Permanova) and in b) dispersion in community composition (Betadisper).

	a) Community composition		b) Dispersion	
Explanatory factor	Pseudo-F_{df}	p	F_{df}	p
Year	**$3.51_{1,62}$**	**0.002**	**$22.46_{1,62}$**	**<0.001**
30m vs Control	$1.26_{1,62}$	0.23	$1.87_{1,62}$	0.178
30mSL vs Control	$1.69_{1,62}$	0.061	$0.70_{1,62}$	0.406
15m vs Control	**$2.32_{1,62}$**	**0.012**	$2.52_{1,62}$	0.119
15mSL vs Control	$1.20_{1,62}$	0.26	$1.78_{1,62}$	0.187
Year*30m vs Control	$0.70_{1,62}$	0.76	$0.13_{1,62}$	0.718
Year*30mSL vs Control	$1.14_{1,62}$	0.33	$1.23_{1,62}$	0.272
Year*15m vs Control	$0.64_{1,62}$	0.82	**$6.63_{1,62}$**	**0.013**
Year*15mSL vs Control	**$2.12_{1,62}$**	**0.014**	$1.31_{1,62}$	0.258

Statistically significant effects (p < 0.05) are indicated in bold.

Table 3 The effects of year, width of the strip, selective logging, and their interactions with Bray-Curtis dissimilarity in a) mean community composition (Permanova) and in b) dispersion in community composition (Betadisper).

	a) Community composition		b) Dispersion	
Explanatory factor	Pseudo-F_{df}	p	F_{df}	p
Year	**$4.08_{1,50}$**	**0.001**	**$18.57_{1,50}$**	**<0.001**
Width	$1.56_{1,50}$	0.091	$2.39_{1,50}$	0.129
Selective logging	$1.13_{1,50}$	0.335	$3.40_{1,50}$	0.072
Year*Width	**$1.90_{1,50}$**	**0.032**	$0.39_{1,50}$	0.538
Year*Selective logging	$0.74_{1,50}$	0.717	**$6.79_{1,50}$**	**0.013**
Width*Selective logging	**$2.26_{1,50}$**	**0.015**	$0.73_{1,50}$	0.398
Year*Width*Selective logging	$0.58_{1,50}$	0.871	$1.55_{1,50}$	0.220

Statistically significant effects (p < 0.05) are indicated in bold.

Figure captions

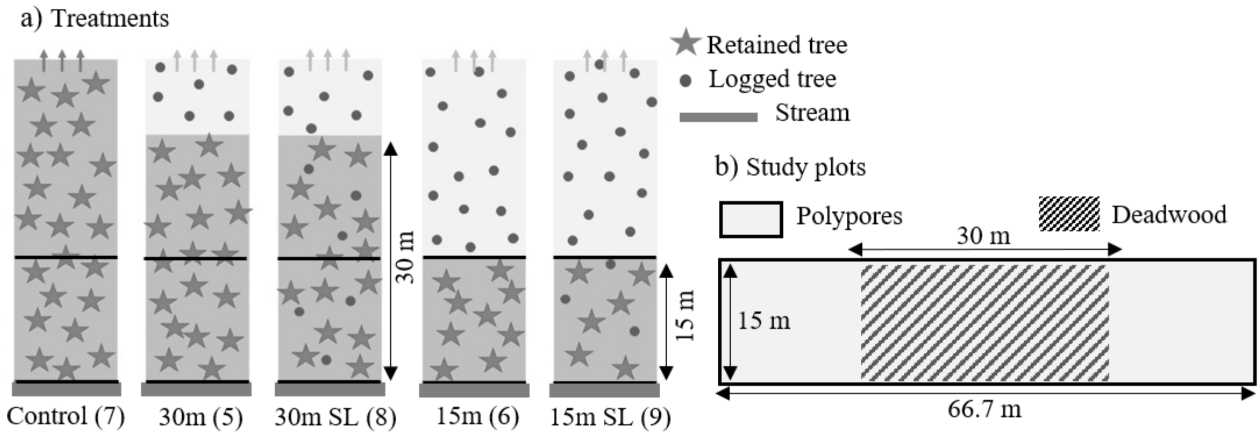

Fig 1. a) Study design of treatments modified from Oldén et al. (2019a). Streams are at the bottom of the figure, arrows above indicate continuous forest cover in the controls and continuing clear-cut area in buffer strip treatments. The treatments are: control, 30 m wide buffer strip with or without selective logging (SL), and 15 m wide buffer strip with or without selective logging. The number of sites per treatment are given in parentheses. b) The study plots for dead wood and polypores.

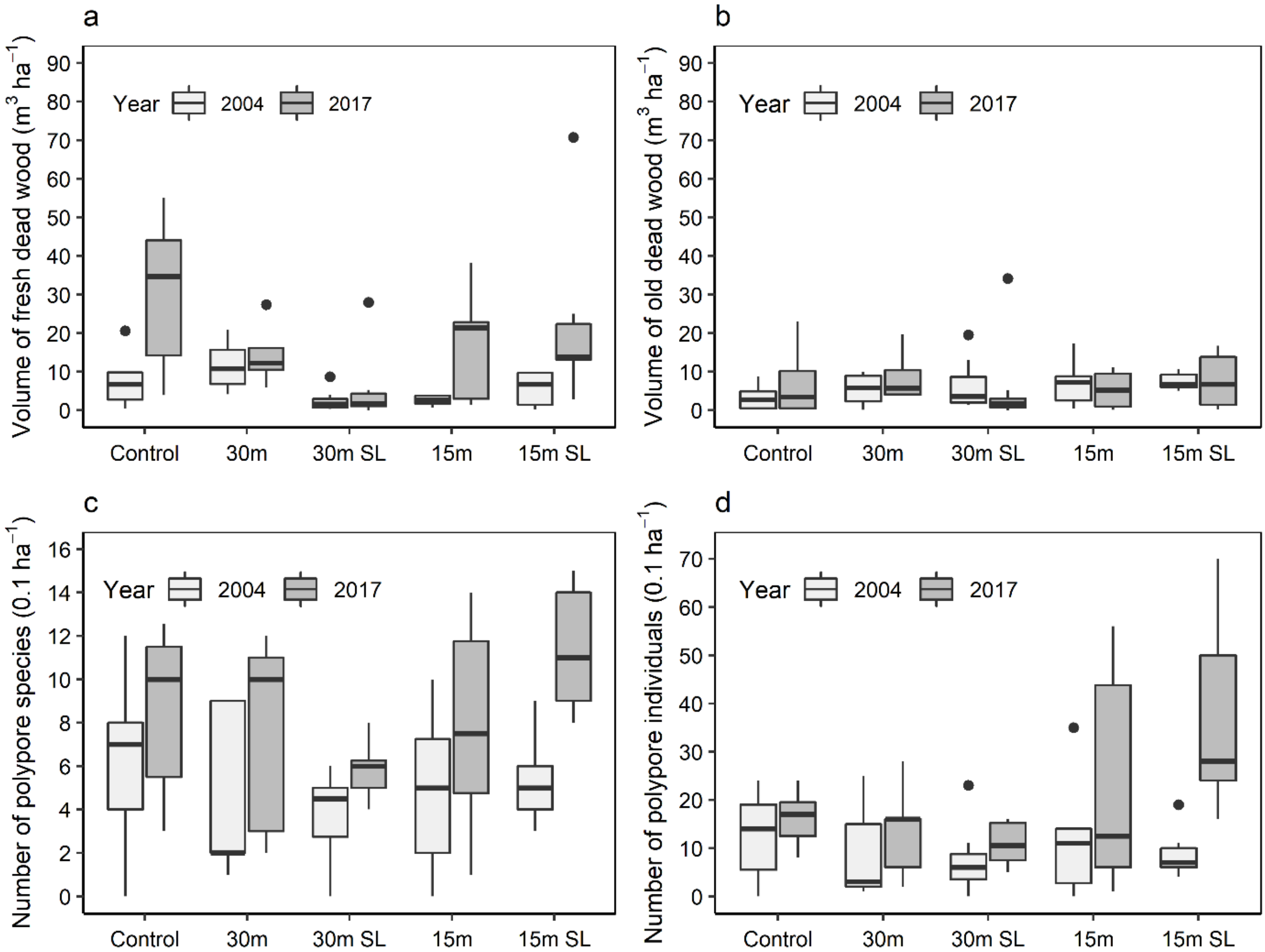

Fig. 2 The volume of fresh dead wood (a), the volume of old dead wood (b), the number of polypore species (c), and the number of polypore individuals (d) on sites of different treatments before the treatment manipulations in 2004 and after the manipulations in 2017. Please note that the scales of y-axis are different in figures c and d. One outlier was removed from the figure b (120 m^3 ha^{-1} in control site 2004).

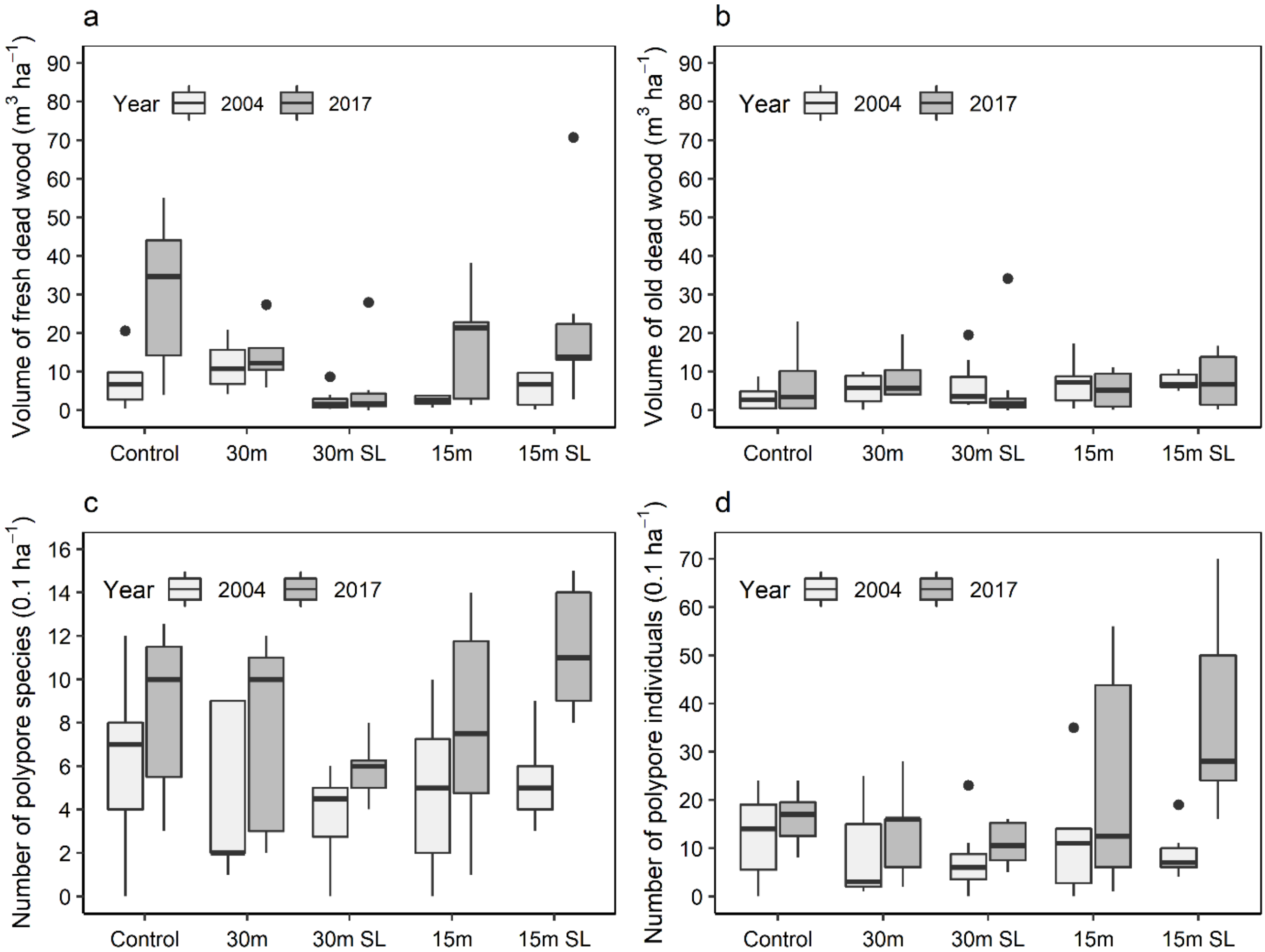

Fig. 3 Non-metric multidimensional scaling plots of polypore species (n=61) communities based on Bray-Curtis dissimilarites (stress=19%). Treatments are indicated by colours. a) Treatment centroids with 95% confidence interval ellipses in 2004 and in 2017 are indicated by dashed and solid lines, respectively. b) Arrows indicate sites, the beginning of the arrow is the composition of the polypore community of the site in 2004 and the end of the arrow is the composition of the polypore community of the site in 2017. Species associated with more than one treatment in 2017 (Table S3) are indicated by black symbols.