Biological legacies buffer local species extinction after logging

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Summary

1. Clearcutting has been identified as a main threat to forest biodiversity. In the last few decades, alternatives to clearcutting have gained much interest. Living and dead trees are often retained after harvest to serve as structural legacies to mitigate negative effects of forestry. However, this practice is widely employed without information from systematic before–after control-impact studies to assess the processes involved in species responses after clearcutting with retention.

2. We performed a large-scale survey of the occurrence of logging-sensitive and red-listed bryophytes and lichens before and after clearcutting with the retention approach. A methodology was adopted that, for the first time in studies on retention approaches, enabled monitoring of location-specific substrates. We used uncut stands as controls to assess the variables affecting the survival of species after a major disturbance.

3. In total, 12 bryophyte species and 27 lichen species were analysed. All were classified as sensitive to logging, and most species are also currently red-listed. We found that living and dead trees retained after final harvest acted as refugia in which logging-sensitive species were able to survive for 3 to 7 years after logging. Depending on type of retention and organism group, between 35% and 92% of the species occurrences persisted on retained structures. Most species observed outside retention trees or patches disappeared.

4. Larger pre-harvest population sizes of bryophytes on dead wood increased the survival probability of the species and hence buffered the negative effects of logging.

5. *Synthesis and applications*. Careful spatial planning of retention structures is required to fully embrace the habitats of logging-sensitive species. Bryophytes and lichens persisted to a higher degree in retention patches compared to solitary trees or in the clearcut area. Retaining groups of trees in logged areas will help to sustain populations of species over the clearcut phase. When possible, old logs should be moved into retention patches to provide a more beneficial environment for dead wood-dependent species. Our study also highlights the need for more before–after control-impact studies of retention forestry to explore factors influencing the survival of species after logging.

Key-words: BACI, conservation, ecosystem recovery, extinction debt, metapopulation dynamics, resilience, structural retention, succession, variable retention harvest

Introduction

Biological legacies in the form of structures and species remaining after a major disturbance are crucial components for the process of ecosystem recovery (Franklin *et al.* 2000). Natural disturbances in forest ecosystems leave large amounts of structures in the form of dead wood but also as surviving trees, especially after low-intensity disturbances (Franklin *et al.* 2002; Kuuluvainen 2009; Swanson *et al.* 2010). This has resulted in unmanaged early successional forests forming a structurally rich environment where these structures serve as substrate both for the species surviving on the disturbed area, but also as valuable target patches for species re-colonization (Swanson *et al.* 2010). Sessile species surviving the disturbance *in situ* may either remain as adult individuals or as

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propagules; for example, vascular plants have the ability to survive disturbance events through seed dormancy in the soil (seed bank) and regenerate after periods of suboptimal conditions, fungal mycelia can survive in leaf litter (Hättenschwiler, Tiunov & Scheu 2005), and lichens and bryophytes (mosses and liverworts) share the ability to stop growing and recover or rejuvenate after disturbance (Green, Sancho & Pintado 2011). Large pre-disturbance population size is likely to positively influence the probability of survival at least in the initial phase. However, since studying these processes requires large-scale systematic before-and-after comparisons, information on this is vastly lacking.

Today, natural disturbances in many parts of the boreal zone have been replaced by clearcutting, an operation leaving very little host substrate for species survival and re-colonization (Kuuluvainen 2009). Different approaches have been adopted to mitigate the negative effects of intensive forestry, and comprise both off- and on-site measures. Nature reserves exemplify off-site approaches while retention of living and dead trees and small areas of intact forest at harvest represent on-site approaches. Retention forestry (synonyms: variable retention, structural retention) has developed during the last few decades and is now commonly applied in different parts of the boreal and temperate forest biomes, and this method is increasingly replacing clearcutting as a harvesting method (Gustafsson *et al.* 2012). A major objective is to 'life-boat' species and processes over the regeneration phase (Franklin *et al.* 2000). Numerous studies have been conducted on the ecological responses to retention forestry (Lindenmayer *et al.* 2012),

including a number of large experiments (Gustafsson *et al.* 2012). One review has been made on the biodiversity effects of retained living trees, largely supporting the life-boating function but also highlighting the need to address the impact on threatened species and over longer time-scales (Rosenvald & Lõhmus 2008).

The main aim of this study was to investigate the factors governing the survival of species after clearcutting, more specifically the role of structural factors such as retention trees and patches (hereafter collectively called retention structures; Fig. 1). We were also interested in the importance of pre-disturbance population size on local species survival. We used forest stands harvested using the retention approach as model system and applied a systematic survey methodology on entire stands before and after logging, using unharvested reference stands as control (before–after control-impact design, BACI; Fig. 1). As model species, we used lichens and bryophytes of conservation concern, classified as particularly sensitive to logging. Apart from constituting major components of boreal forest biodiversity, bryophytes and lichens are both poikilohydric organisms meaning that they lack water-regulating mechanisms (Proctor 1982), making them the ideal study organisms to monitor the effect of changes in local environmental conditions.

Our main hypotheses were as follows: (i) species of conservation concern survive to a larger extent on retention structures than on the clearcut areas and (ii) a large local pre-disturbance population size positively affects the degree of survival after logging. As one of very few before-and-after studies on red-listed species in two very species-
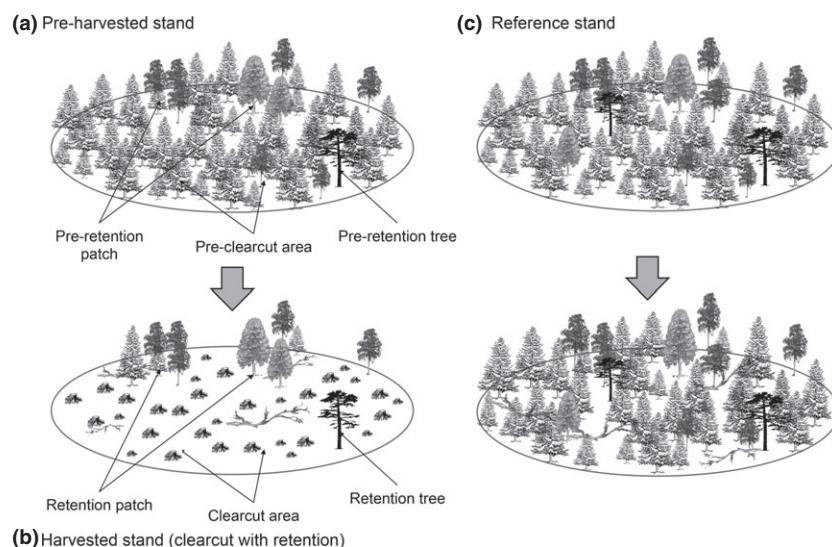

Fig. 1. Before–after control-impact design (BACI) and terminology used in this study. (a) Pre-harvested stand (before clearcutting with retention), showing pre-retention patches (areas to become retention patches), pre-clearcut areas (areas to become clearcut) and pre-retention trees (dispersed, individual living trees to become retained in the harvested stand, that is, outside retention patches). (b) Harvested stand (clearcut with retention), showing retention patches (groups of living and dead trees retained in the harvested stand), clearcut areas (the open surface of a harvested stand without retention structures) and retention trees (solitary, living trees retained in a harvested stand, that is, outside retention patches). Solitary retention trees and patches were collectively called retention structures after clearcutting and pre-retention structures before clearcutting. (c) Reference stand (unharvested control stand).

rich groups, and also by providing far more detail than previous studies by following 499 species occurrences from before logging and 3 to 7 years after logging, this study provides important information for this area of conservation research. It is the first study that adopts a methodology that enables monitoring of location-specific substrates.

Materials and methods

FOREST STANDS

The forest stands were situated within an area of 4700 km^2 in the county of Gävleborg, Sweden, on the land of the forest company Holmen Skog. The area lies in the transition zone between the southern and middle boreal vegetation zones (Ahti, Hämet-Ahti & Jalas 1968) with its central point at 16°30′E, 61°57′N. The survey stands were initially chosen in 2002 as an appropriate representative of spruce-dominated stands soon to be harvested (Gustafsson *et al.* 2004). About 80 stands comprising c. 700 ha met the required criteria in 2002: (i) mature to be logged, (ii) age >110 years, (iii) size >3 ha and <16 ha, (iv) altitude <400 m a. s. l., (v) relative basal area of *Picea abies* (L.) Karst >70%, (vi) site quality >G20 (indicating that a 100-year-old *P. abies* tree reaches the height of more than 20 m), (vii) vegetation of dwarf shrub or low herb type and (viii) soil-moisture-type mesic or moist. From the stands that met all criteria, 30 were randomly selected in 2002. Gustafsson *et al.* (2004) give a more detailed description of the initial stand characteristics.

SPECIES INVENTORIES

With the aim of evaluating changes in the occurrence of bryophytes and lichens of conservation concern, in this context defined as species classified as red-listed in the Swedish Red List of 2000, 2005 or 2010 (Gärdenfors 2000, 2005, 2010), all 30 stands were revisited in 2010. Twelve stands remained unharvested (hereafter referred to as 'reference stands'), and 16 stands were clearcut with retention 3 to 7 years prior to our second survey. Retention of solitary trees and tree groups was performed, prioritizing old and dead trees, and uncommon habitats with high frequency of deciduous trees or dead wood. Importantly, the forestry planners had no prior knowledge about the red-listed species occurrences from the first survey in 2002. Two selectively harvested stands were omitted from the study due to the unconventional harvesting methods which were applied. For the re-inventory, we utilized two different survey methods: (i) stand-level inventories according to the methods of Gustafsson *et al.* (2004) and (ii) location-specific re-inventories of individual species observations utilizing the data collected in 2002 (Gustafsson *et al.* 2004). The fieldwork was conducted in May–August 2002 and June–September 2010. The same surveyors carried out the lichen inventory in both years, whereas different persons surveyed the bryophytes in 2002 and 2010, respectively. By standardizing the recording effort between years and also by using unharvested controls, we minimized the effect of bias due to the differences in surveyor skills. Species that were difficult to determine in the field were collected and subsequently determined in the laboratory under dissecting microscopes. The lichens *Alectoria sarmentosa*, *Bryoria nadvornikiana*, *Micarea globulosella* and the bryophyte *Lophozia ciliata* were so abundant that, given the time limit, they were omitted from the

inventory already in 2002. The nomenclature follows Santesson *et al.* (2004) for lichens and Hallingbäck, Hedenäs & Weibull (2006) for bryophytes.

In stand-level inventories (before and after logging, with unharvested controls; Fig. 1), the surveyors walked in adjacent parallel 10-m-wide belts covering the whole surface of each stand. They kept direction with the use of compass, aerial photographs and by locating stand borders with GPS coordinates. All substrates above the ground and up to 2 m high were surveyed. When a species was found, a 10 m × 10 m square was delimited, with the observation in the centre, and any additional species within the square were recorded. Thus, there could only be one observation of a particular species, but several species observations in total within a 10 m × 10 m square. All observations were assigned a 'dominant' host substrate and a square-centred GPS position. For all dominant tree substrates, the surveyors recorded species (when possible), diameter at breast height (dbh, in cm) and status (living tree, high stump, snag or log). The surveyors recorded if the species occurred in retention structures or on clearcut areas (on cut stumps, logs or small trees with a dbh <10 cm in sun-exposed locations outside of retention patches). The size and location of the retention structures were cross-validated against aerial photographs using GIS (applying a 5-m error margin around retention patches; spatial resolution of the aerial photographs was 0·5 m per pixel). In clearcut areas, the surveyors recorded whether the substrate where the species was found had been cut or otherwise harmed during final felling. Three plot-level (10 m × 10 m) frequency of occurrence classes were estimated for each species observation: 1 = <5 crusts per thalli per thufts or colonies with coverage area <10 cm^2; 2 = 5–100 crusts per thalli per thufts or colony coverage area 10–400 cm^2; and 3 = >100 crusts per thalli per thufts or colony coverage area >400 cm^2.

In a location-specific species re-inventory (performed directly after the stand-level inventory of each stand in 2010), the surveyors utilized aerial photographs, substrate characteristics and GPS coordinates with species observation data from 2002 to retrieve individual species observations and host substrates to reassess their status (living or dead/absent). The surveyors recorded whether the species occurred on dispersed living retention trees or within retention patches. The confidence in each reassessed observation was described as 1 = very certain, 2 = certain and 3 = very uncertain. The observations classified as 'very uncertain' were omitted from any subsequent analyses. The location-specific species re-inventory revealed that many lichen observations in 2002 were missed during the 2010 stand-level inventory after logging. Based on this, the average detection error (i.e. mean number of undetected species observations ha^{-1} between the 2010 stand-level inventory and the location-specific species re-inventory) was 0·65 observations ha^{-1} for lichens in reference stands, 0·11 observations ha^{-1} for clearcut areas and 0·29 observations ha^{-1} for retention structures. We added these error estimates to the observed number of occurrences in the analyses. The bryophyte data needed no adjustment for detection errors.

DATA ANALYSIS

Stand-level inventories before and after logging

Cumulative species richness. We performed sample-based rarefaction curves (Gotelli & Colwell 2001) using EstimateS version

8.2.0 (Colwell 2006) for comparisons of bryophyte and lichen species richness in clearcut areas, retention structures and reference stands, respectively, prior to harvest in 2002 and after harvest in 2010. Species observations and habitat area were pooled within stands. We rescaled the *x*-axis to represent cumulative habitat area since the amount of habitat surveyed differed between stands. We visually compared species richness curves and associated confidence interval curves, at comparable levels of sampling effort, that is, at an equal cumulative area sampled. Differences in species richness were considered non-significant ($P > 0.05$) if confidence intervals overlapped (Colwell, Mao & Chang 2004).

Species observations. We used the Wilcoxon test to test for differences in number of bryophyte and lichen observation per ha between clearcut areas and retention structures in paired harvested stands and reference stands, respectively, in 2002 and 2010. We used the Mann–Whitney *U*-test suitable for unbalanced sampling to test for differences between the three types, clearcut areas, retention structures and reference stands. All reported *P*-values are two-tailed.

Location-specific species re-inventory

Species survival. To explore bryophyte and lichen survival in known specific locations in harvested and reference stands, we used multiple regression models including the explanatory variables: time since harvest (number of years), the habitat type after harvest (retention structures or clearcut area), 2002 frequency of occurrence class, tree-species category (coniferous or deciduous) and tree dbh. Since there were few frequency of occurrence class 3 observations, we pooled class 2 and class 3, whereby this variable was treated as a response where index $0 = <5$ crusts per thalli per thufts or < 10 cm^2 colony coverage, and index $1 = >5$ crusts per thalli per thufts or > 10 cm^2 colony coverage. We chose not to split the category 'retention structures' into 'retention patch' and 'solitary retention tree' since too few observations were made for each group. The binary response variable survival was defined as the bryophyte or lichen being present (1) or absent (0). We considered each absence as a local species extinction event, with underlying causes such as succession, sun exposure, substrate loss or damage inflicted during harvest. We used generalized linear mixed models (GLMMs) with stand as random factor (letting the coefficients vary by stand as a means of dealing with non-independence of the data), defined using a binomial distribution of errors and logit link function (e.g. Bolker *et al.* 2009). We ran separate models for bryophytes and lichens occurring on dead and living trees in harvested stands and reference stands, respectively. Bryophyte and lichen species identity (only including species with ≥7 observations) was initially included as an explanatory variable in the analyses, but this had no significant effect on survival and so species were pooled for dead and living trees. Number of species observations on other types of substrates such as the ground and boulders were low and subsequently not analysed (see Table S1 in Supporting Information). A total of eight global models were defined. Once the global models were defined, we standardized the input variables using Gelman's (2008) approach, using the standardized function available within the R package arm (Gelman *et al.* 2012). No explanatory variables were strongly correlated.

We used model averaging to assess the relative strength of support for all biologically considerable models, as recommended when the Akaike weights (wi) of the 'best models' was < 0·9 (Grueber *et al.* 2011). In cases where two or more models achieve similarly high levels of support, model averaging of this 'top model set' can provide a robust means of obtaining parameter estimates (Burnham & Anderson 2002). The Akaike weight of a model is essentially its probability compared to the probability of the other plausible models, and the sum of the Akaike weights for all plausible models is 1. Hence, we used an information theoretic or 'IT' approach for model selection, calculating Akaike's Information Criterion adjusted for small sample size (AICc) and Akaike weights in the R package MuMIn (Barton 2011). We defined the top model set through applying a cut-off value of ΔAICc < 5 (Barton 2011). We followed the methodological guidelines and IT approach of Grueber *et al.* (2011), recognizing that the handling of random effects in the IT environment has not to date been fully resolved. To provide values for the goodness-of-fit for the GLMMs, conditional and marginal R^2 values were calculated. The conditional R^2 value shows the proportion of the variance in the raw data explained by the full model, including both fixed and random effects, while the marginal R^2 value shows the proportion of the variance explained by the fixed effects only. We used the statistical software R 2.13.0 (R Development Core Team) and the add-on package lme4 (Bates & Maechler 2011).

Results

CLEARCUT AREAS AND RETENTION STRUCTURES

Retention structures (patches and individual trees) were mapped and quantified in all harvested stands (Table 1), averaging 9·7 dispersed living trees per ha and 0·83 ha (12% of total stand area) of retention patch area per stand. In 2010, a total of 168 observations of 8 bryophyte species were made in the 16 harvested stands compared with 369 observations of 10 species in the 12 reference stands (Table 2). Most bryophytes (69%) occurred on logs. We recorded 122 observations of 18 lichen species in harvested stands and 269 observations of 20 species in reference stands, with a majority on living trees (Table S1). The majority of the observations in harvested stands were made on retention structures, 86% of all bryophytes and 92% of all lichens.

STAND-LEVEL INVENTORIES BEFORE AND AFTER LOGGING

Cumulative species richness

Rarefaction curves showed that the bryophyte and lichen species richness before harvest did not differ significantly between pre-clearcut areas, pre-retention structures and reference stands (Fig. 2a and c). Rarefaction curves for bryophyte richness revealed significantly lower species richness in clearcut areas compared with reference stands, but no significant difference between clearcut areas and retention structures (Fig. 2b). Lichen species richness was

Table 1. Mean, standard deviation (in parentheses) and range (in italics) of stand characteristics. All values except time since harvest, number of retention trees ha^{-1}, retention patch area (ha and proportion of stand) represent the pre-harvest conditions (2002) from the forest owner (Holmen Skog) data base

	Harvested stands	Control stands
Size (ha)	6·4 (3·8) *3·2–15·8*	5·0 (1·6) *3·3–8*
Altitude (m above sea level)	257·8 (83·3) *50–370*	254·2 (84·9) *40–370*
Age (years)	119·8 (11·9) *110–147*	121·9 (9·8) *111–144*
Number of stems ha^{-1}	897·4 (176·2) *662–1337*	979·8 (167·7) *658–1354*
Volume (m^3 ha^{-1})	325·1 (59·8) *235·5–473·2*	312·1 (44·8) *251·1–409·8*
Proportion Scots pine, *Pinus sylvestris* (%)	10·0 (8·2) *0–20*	10·0 (7·4) *0–20*
Proportion Norway spruce, *Picea abies* (%)	78·1 (8·3) *70–90*	78·3 (5·8) *70–90*
Proportion deciduous trees (%)	11·9 (4·0) *10–20*	11·7 (3·9) *10–20*
Time since harvest (years)	4·69 (1·35) *3–7*	
Number of retention trees ha^{-1}	9·69 (9·23) *1·7–40·8*	
Retention patch area (ha)	0·83 (0·78) *0·03–2·84*	
Proportion retention patch area (% of stand)	12·35 (9·76) *1·0–31·1*	

Table 2. Bryophyte and lichen species observations on clearcut areas (cc) and retention structures (ret) in 16 harvested stands and 12 unharvested reference stands (ref) in 2002 and 2010, data from stand-level inventories (SLI) and location-specific re-inventories (LSRI) of individual species occurrences. Location-specific re-inventory data include only observations that are 'certain' or 'very certain' (see Materials and methods). More detailed information on the species and their main substrates is given in Table S1

Species group	SLI-2002			SLI-2010			LSRI-2010		
	Pre-cc	Pre-ret	Ref	Cc	Ret	Ref	Cc	Ret	Ref
Bryophytes	228	141	205	24	144	369	2	69	121
Lichens	224	65	202	10	110	269	7	32	110

significantly lower in clearcut areas compared to both retention structures and reference stands (Fig. 2d).

Species observations

The number of bryophyte and lichen observations ha^{-1} did not differ significantly between pre-harvested stands and reference stands in 2002 ($U > 67$, $P > 0.18$; Fig. 3a). However, pre-clearcut areas as well as clearcut areas hosted significantly lower species densities than retention structures ($Z > 2.637$, $P \leq 0.010$; Fig. 3b). Pre-clearcut areas in 2002 hosted significantly higher species densities of both bryophytes and lichens compared with clearcut areas in 2010 ($Z > 3.237$, $P < 0.002$; Fig. 3b). Bryophyte species densities increased in reference stands from 2002 to 2010 ($Z = 3.059$, $P = 0.002$; Fig. 3a).

Location-specific species re-inventory

In total, 103 observations of *Orthotrichum gymnostomum* from 2002 were reassessed with certainty in nine harvested stands, with 30 occurrences (29%) persisting after harvest, 17 in retention patches and 13 on solitary retention trees. The survival of *O. gymnostomum* in retention patches was on average 92% and on solitary retention trees was 78%. The best-supported model of survival in harvested stands ($w = 0.33$; Table S2) included the retention of Aspen *Populus tremula* L. (high relative importance $\Sigma = 1.0$; Table 3). Five models including frequency of occurrence in 2002, time since harvest and dbh made up the remaining model weights (see Table S2). We found no significant effect of frequency of occurrence in 2002, time since harvest or dbh (confidence intervals included zero) on survival. In comparison, 33 occurrences out of 40 (83%) were retrieved with certainty in reference stands ($n = 9$). For *O. gymnostomum* in reference stands, the null model was included in the set of candidate models. Results for this species were therefore judged as unreliable and are not shown.

Of all bryophyte observations on dead wood from 2002 (most commonly of *Anastrophyllum hellerianum*, *Calpogeia suecica*, *Lopozia ascendens* and *Lopozia longiflora*), 184 observations were reassessed with certainty in 2010 in 13 harvested stands, of which 31 occurrences (on average 21%) persisted after harvest. Inside retention patches, on average 56% of the bryophyte occurrences persisted, whereas the corresponding proportion outside retention patches was only 11%. Retention structures ($\Sigma = 1.0$) and a high frequency of occurrence in 2002 ($\Sigma = 0.92$) had strong explanatory power for bryophyte survival on deadwood. Although the confidence intervals included zero, increasing time since harvest had 56% relative importance (Σ) compared to retention and frequency class (negative effect on survival, Table 3). Notably, the surveyors classified substrate damage as the main reason for bryophyte species loss on deadwood (in 69% of cases). Compared with harvested stands, bryophyte survival on deadwood in reference stands was approximately three times as high,
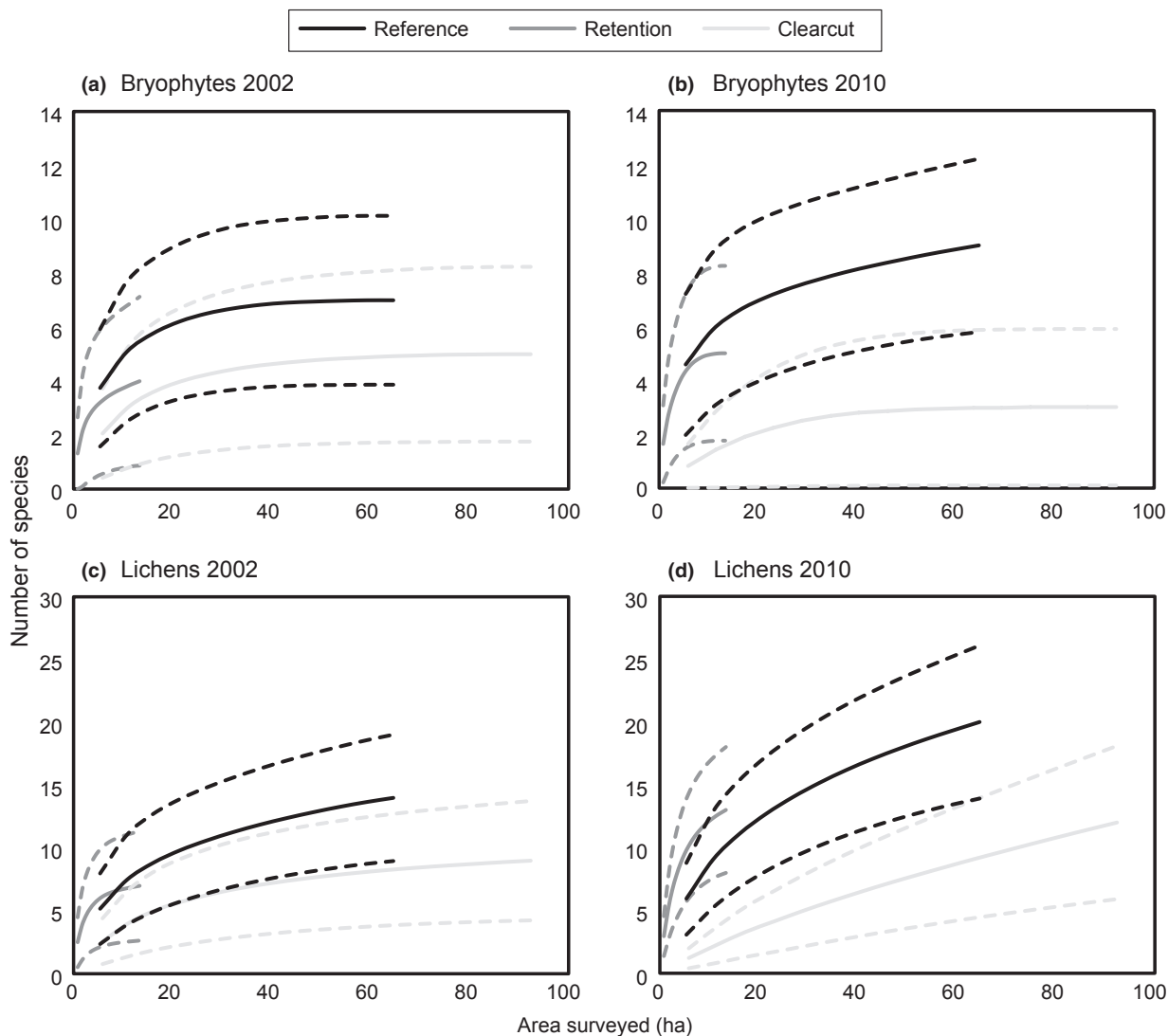
Fig. 2. Rarefaction curves for the comparisons of (a–b) bryophyte and (c–d) lichen species richness in clearcut areas, retention structures (retention) and reference stands prior to harvest in 2002 and after harvest in 2010. Dashed lines = 95% confidence intervals.

where 81 of 151 (54%) occurrences persisted from 2002 to 2010. Increasing tree diameter had a positive effect ($\Sigma = 1\cdot0$) on species survival in the reference stands. Species on deciduous logs had somewhat higher survival probability (75% relative importance to dbh), although not significant (Table 3). This was probably the result of the relatively low proportion (37%) of persistence of *L. longiflora* on coniferous logs.

We reassessed 157 lichen observations from 2002 (including species such as *Arthonia incarnata*, *Biatora ocelliformis*, *Cheiromycina flabelliformis*, *Cliostomum leprosum* and *Lecanora impudens*) with certainty in 2010 on living trees in 15 harvested stands, and of these, 33 (on average 29%) persisted after harvest. In retention patches, on average 48% of the lichen occurrences persisted, and on solitary retention trees, 35% persisted. Retention structures had the greatest relative positive influence on lichen survival ($\Sigma = 1\cdot0$). In reference stands, 111 lichens were

reassessed, where 75% were still alive in 2010 (Table 3). The sample size of lichens on deadwood in harvested stands was too small to model; only four observations out of 53 (8%) were alive in 2010 (all in retention). In reference stands, 26 lichens out of 57 on deadwood were alive in 2010 (46%). Frequency class $2 + 3$ ($\Sigma = 1\cdot0$) had the greatest relative positive effect on lichen survival on deadwood in these stands.

Discussion

The main result from our study was that living and dead trees retained at final harvest increased survival of species classified as sensitive to forestry, compared to traditional clearcutting. Survival after logging was significantly higher for bryophytes as well as lichens on retained structures than on clearcut areas, and thus, our first key hypothesis was supported. For bryophytes living on dead
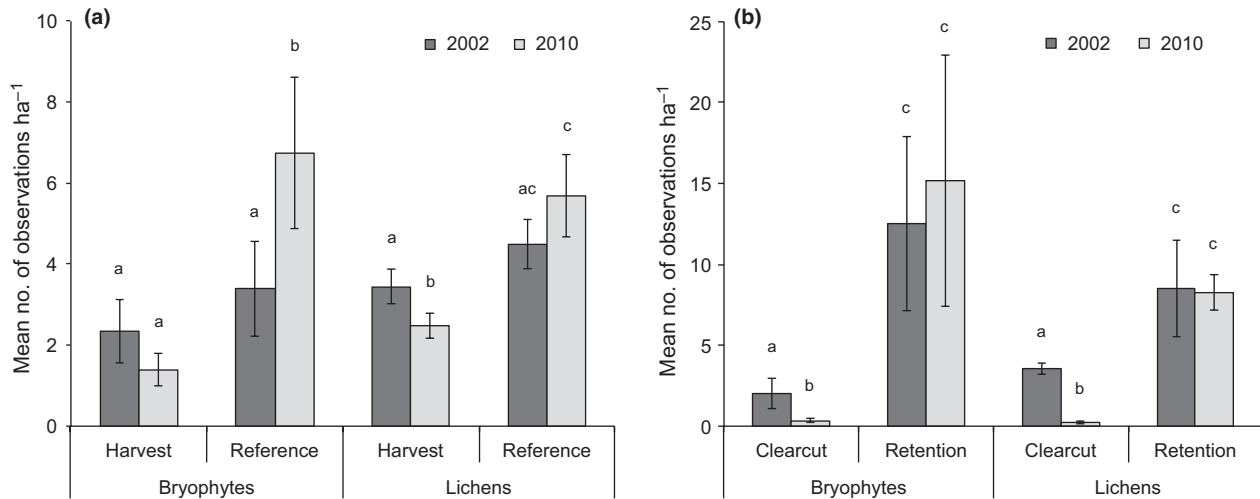
Fig. 3. (a) Mean number of observations ha^{-1} (±SE bars) of bryophytes and lichens of conservation concern in harvested stands ($n = 16$) and reference stands ($n = 12$) in 2002 and 2010, respectively. (b) Mean number of observations ha^{-1} (±SE bars) of bryophytes and lichens of conservation concern in clearcut areas and retention structures (= retention) prior to harvest in 2002 and after harvest in 2010, respectively. Means sharing the same letter are not significantly different at $P > 0.05$ (considering each taxonomic group separately).

wood, our second key hypothesis was also supported since strong pre-harvest populations in this guild impacted positively on resistance to logging disturbance. Results align with previous studies on the life-boating effect; in a review on green-tree retention, Rosenvald & Lõhmus (2008) concluded that in more than 70% of analysed studies, the harvest-related loss of species and populations was lowered. Common practice in biodiversity studies on retention forestry has been to survey only after logging (e.g. Hedenås & Hedström 2007; Perhans *et al.* 2009; Pharo & Lindenmayer 2009). Our study is the first to analyse location-specific re-inventory data on two species-rich forest organism groups. Hylander & Weibull (2012) studied species composition in buffer strips along streams, but they only studied bryophytes and mainly focussed on common species. Also novel to our study was that our methodology, using a two-step re-inventory, enabled us to take any detection error into account. It also allowed us to follow the development in unharvested reference stands – where we found an increase in number of observations of many species, especially among bryophytes. A general problem with before and after studies is that surveyor skills may change over time, but by including reference stands (control treatment) in our study, we could control for this. It is unlikely that the observed increase in number of bryophyte observations in reference stands is due to differences in pre-harvest conditions since stand variables had very similar values (Table 1). A possible explanation to the increase might be differences in surveyor skills between 2002 and 2010. Another explanation may be the longer exposure time of the forest to dispersal propagules, but also potentially a longer time to build up a higher richness of suitable microhabitats.

SPATIO-TEMPORAL ASPECTS OF SURVIVAL AND EXTINCTION

Our study highlights two key processes after a major disturbance such as clearcutting: extinction and survival. It is likely that some species remaining on the cut area (mainly on dead wood) are experiencing a local extinction debt, that is, they are doomed to disappear from the area before the forest canopy closes. Our study shows that retention of dead and living trees moderates the negative effects of logging by increasing the rate of survival of logging-sensitive species in the short term. From previous studies, we know that logging-sensitive species do occur near north-facing forest edges c. 20–25 years after clearcutting (Caruso, Rudolphi & Rydin 2011), but that such positive edge effects may not be detectable after c. 40 years (Hylander 2009; Rudolphi & Gustafsson 2011). However, before this study, it was not clear to what extent survival due to the retention of substrates is responsible for the presence of these species in young forest stands after logging. The other possible explanation would be re-colonization from surrounding forests, but our study clearly indicates that *in situ* survival may in fact be underestimated in previous studies (e.g. Hylander 2009). With the location-specific approach, our study provides stronger evidence that the species are actually surviving inside the retention patches. Hylander *et al.* (2005) showed that red-listed bryophyte species may survive after logging in retention patches, but they did not apply a location-specific approach and only buffer strips along streams were included, being not entirely representative for upland conditions (Dynesius, Hylander & Nilsson 2009).

Bryophytes were generally more sensitive to the clearcutting disturbance, agreeing with other studies (e.g. Perhans *et al.* 2009). A possible explanation is that most

Table 3. Variables explaining survival of bryophytes and lichens of conservation concern in harvested and unharvested reference stands. Summary results of the standardized effect sizes resulting after model averaging. Shown are average parameter estimates, standard errors (SE), 95% confidence intervals (CI) and relative variable importance (Σ) of the explanatory variables on the survival of bryophytes and lichens on living and dead substrates in harvested and reference stands. Positive estimates indicate higher survival, and significant variables (not including zero in the 95% CIs) are marked in boldface

Model average parameters	Estimate*	SE	95% CI Lower	95% CI Upper	$\Sigma^\dagger$
Harvested stands					
Orthotrichum gymnostomum on living trees					
Marginal R^2 = 0·73 and conditional R^2 = 0·75					
(Intercept)	−4·725	1·259	−7·192	−2·258	
Dbh	0·445	0·880	−1·280	2·170	0·22
Frequency class > 1	1·140	1·014	−0·847	3·127	0·40
Retention structures	**6·057**	**1·243**	**3·622**	**8·493**	**1·00**
Time since harvest	0·913	1·272	−1·581	3·407	0·24
Bryophytes on dead trees					
Marginal R^2 = 0·67 and conditional R^2 = 0·74					
(Intercept)	−7·174	1·721	−10·547	−3·801	
Dbh	0·502	0·722	−0·914	1·917	0·30
Frequency class > 1	**2·631**	**1·325**	**0·033**	**5·228**	**1·00**
Retention structures	**5·801**	**1·017**	**3·808**	**7·795**	**0·92**
Deciduous	1·066	0·967	−0·829	2·960	0·34
Time since harvest	−1·528	0·908	−3·309	0·252	0·56
Lichens on living trees					
Marginal R^2 = 0·42 and conditional R^2 = 0·42					
(Intercept)	**−2·877**	**0·531**	**−3·917**	**−1·836**	
Dbh	0·377	0·479	−0·560	1·317	0·28
Frequency class > 1	0·460	0·502	−0·524	1·444	0·33
Retention structures	**2·943**	**0·509**	**1·945**	**3·940**	**1·00**
Deciduous	−0·004	0·662	−1·301	1·294	0·23
Time since harvest	0·786	0·492	−0·178	1·750	0·0·58
Reference stands					
Bryophytes on dead trees					
Marginal R^2 = 0·13 and conditional R^2 = 0·15					
(Intercept)	0·030	0·266	−0·492	0·552	
Dbh	**1·135**	**0·376**	**0·398**	**1·871**	**1·00**
Frequency class > 1	0·085	0·399	−0·697	0·867	0·19
Deciduous	0·812	0·423	−0·017	1·641	0·75
Lichens on living trees					
Marginal R^2 = 0·09 and conditional R^2 = 0·17					
(Intercept)	**0·815**	**0·366**	**0·097**	**1·533**	
Dbh	0·767	0·544	−0·299	1·833	0·56
Frequency class > 1	0·888	0·544	−0·053	1·829	0·78
Lichens on dead trees					
Marginal R^2 = 0·33 and conditional R^2 = 0·33					
(Intercept)	−0·333	1·395	−3·047	2·381	
Dbh	0·715	0·941	−1·130	2·560	0·34

Table 3. (continued)

Model average parameters	Estimate*	SE	95% CI Lower	95% CI Upper	$\Sigma^\dagger$
Frequency class > 1	**1·764**	**0·688**	**0·416**	**2·565**	**1·00**
Deciduous	−1·861	1·197	−4·207	0·486	0·61

*Effect sizes have been standardized on two SD following Gelman (2008).

$\dagger$The relative importance (Σ) for an explanatory variable is the sum of Akaike weights of the models in which the variable was present.

bryophyte species in our study were growing on dead wood and that decay processes between 2002 and 2010 resulted in deterministic extinctions. Conversely, most lichens, such as *Biatora ocelliformis*, were found on living trees and had relatively high survival, also agreeing with responses found by Perhans *et al.* (2009). The high epiphytic survival of lichens, but also the bryophyte *O. gymnostomum*, agrees with the patch-tracking metapopulation model in which species are assumed to remain on its substrate until the substrate is deterministically destroyed (Snäll, Ribeiro & Rydin 2003).

On clearcut areas, the microclimatic conditions are dramatically different compared to the closed forest with higher temperature fluctuations and wind velocities (Chen, Franklin & Spies 1993) and retention levels of c. 15% does very little to enhance the average conditions (Heithecker & Halpern 2006). Species growing on convex substrates (e.g. logs, tree stumps, living and dead standing trees) have been suggested to be especially vulnerable to the change in microclimate following clearcutting (Hylander *et al.* 2005). In our study, more species on solitary retention trees survived after logging than species found on woody debris. Our study suggests that the biologically relevant conditions within the retention patches may be comparable with the conditions inside closed forests when it comes to survival of logging-sensitive species of bryophytes and lichens.

APPLICATION FOR PRACTICE

Our findings support the retention approach as an efficient way to increase persistence of pre-harvest species after clearcutting. In retained structures, even more observations were made after than before harvest. It is important to remember that the retention levels in our study are higher than the mean from the country as a whole (3–5% of harvested area; Gustafsson *et al.* 2012), implying that benefits arising from retention might be higher in our study than on stands with lower retention levels. Preserving forest patches as well as individual trees on clearcuts also provides a long-term measure to create

microreserves spread over forest production landscapes, which complement traditional conservation areas such as nature reserves and national parks. Our model species were all nationally uncommon, disturbance sensitive, sessile and highly substrate specialized, that is, we worked with highly vulnerable biodiversity. This means that other, less-vulnerable forest-interior species are likely to show weaker, or at most a similar response. Nevertheless, colonization of new substrates is also a prerequisite for future long-term survival of common species associated with transient habitats such as living trees and dead wood.

Our study shows that clearcutting has severe negative effects on the survival possibilities for many rare and threatened species. For logging-sensitive species living on exposed substrates such as woody debris and standing trees, these negative effects may be mitigated through carefully planned retention actions, for example by placing retention tree groups where these species are aggregated. A possibility to further optimize the environmental conditions of retention structures is to leave them close to north-facing edges, which has been shown to be more beneficial than retention in exposed south-facing edges (Rudolphi & Gustafsson 2011). In our study, substrate destruction was identified as the main factor causing the disappearance of bryophyte species on dead wood. For these species, moving logs into retention patches instead of leaving them on the exposed clearcut area could help to reduce light exposition and avoid damage from machine operations including slash harvest for bioenergy purpose and soil scarification (Hautala *et al.* 2004; Rudolphi & Gustafsson 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. List of bryophyte and lichen species observations.

Table S2. Submodels included in our model averaging approach.