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Epixylic, forest-interior bryophytes in young stands - importance of local environmental variables, propagule sources, and distance to bordering woodland key habitats

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Populärvetenskaplig sammanfattning

2010 slutavverkades 170 000 ha skog i Sverige. Det är en yta som är bra mycket större än Öland. Stubbarna som blir kvar utgör en stor del av den totala mängden död ved i dagens produktionsskogar.

Jag har genom min studie visat att mossor som lever på död ved (vedlevande), som man normalt bara associerar med gamla skogar (bl.a. den rödlistade vedtrappmossan och fridlysta grön sköldmossa), också kan leva på stubbar och annan grov död ved i ungskogar nära så kallade nyckelbiotoper. Nyckelbiotoper är områden i produktionsskogen som skogsstyrelsen har pekat ut som extra värdefulla för rödlistade arter. De innehåller ofta strukturer som påminner om naturskogar, t.ex. mycket död ved. Sådan information som min studie har gett kan visa sig vara värdefull. Stubbar är nämligen aktuella just nu. Eftersom jakten på koldioxidneutral energi hela tiden ökar riktas nu blickar mot stubbskörd, dvs. att man rycker upp stubbar med rötterna efter att träden är avverkade och använder veden till bioenergi. Tar man upp stubbarna riskerar man dessutom att förstöra annan grov död ved vid skörden. Förra året anmäldes 5010 ha för planerad stubbskörd och det är en siffra som med stor sannolikhet kommer att öka kommande år. Därför pågår forskning vid SLU i Uppsala för att utreda positiva och negativa effekter av en storskalig stubbskörd.

Grov död ved är en stor bristvara i den moderna produktionsskogen. I en naturskog dör gamla träd kontinuerligt och det skapas en jämn tillgång på död ved för sådana organismer som kräver det för sin överlevnad. Men eftersom träden i en produktionsskog avverkas långt innan de naturligt skulle dö bryts den naturliga, kontinuerliga tillförseln av död ved. Istället skapas tillfälligt stora mängder genom de grenar och stubbar som blir kvar på ett kalhygge efter en slutavverkning, för att sedan minska kraftigt när skogen blir äldre. Denna minskning och förändring av den döda veden har orsakat att hälften av Sveriges rödlistade arter är sådana som är beroende av död ved. Det finns nämligen mängder av organismer som kräver död ved för sin överlevnad. Några grupper där det finns många vedlevande arter är insekter, mossor, svampar och lavar.

Även om stubbar och annan död ved som skapas vid slutavverkning alltså inte har kommit till naturligt kan den ändå vara viktig p.g.a. att det inte finns så mycket annan död ved att välja på. Om man kan ta reda på under vilka förutsättningar stubbar kan vara värdefulla för ovanliga vedlevande arter kan man undanta dessa från stubbskörd. En stubbskörd som tar hänsyn till bl.a. vedlevande organismer på ett sådant sätt att de viktiga stubbarna sparas behöver inte vara negativ och kan möjligtvis bidra till att öka andelen koldioxidneutral energi. Men då måste vi ta reda på var de viktiga stubbarna finns så att dessa kan skyddas. Min slutsats är att stubbar i närheten av nyckelbiotoper kan hysa vedlevande arter som missgynnas av det moderna skogsbruket och att de därför bör undantas från stubbskörd.

Abstract

The reduction of coarse, dead wood is considered to be the biggest threat to flora and fauna in boreal forests. Extensive harvest of logging residues would increase this reduction even more. However, the role of dead wood created at final felling for boreal, epixylic species is still largely unclear. It is therefore of interest to examine whether epixylic species inhabit the dead wood in young, boreal stands, especially species considered to be confined to forests in late successional stages.

The aim of this study was to investigate whether forest-interior species in fact can inhabit early-successional forests arisen after logging. The study was conducted in young stands bordering dead wood rich woodland key habitats. All CWD and totally 202 FWD in five plots were searched for the presence and abundance of the study species, and local environmental variables, propagule sources and distance to bordering woodland key habitats were recorded. The effects of the variables on the presence and abundance of five forest-interior epixylic bryophytes, (*Anastrophyllum hellerianum*, *Buxbaumia viridis, Herzogiella seligeri, Lophocolea heterophylla* and *Nowellia curvifolia*) were analysed. For comparison epixylic bryophytes and lichens considered to be open-forest species and generalist species was also included.

Predictive models could be built for the abundance of *A. hellerianum* and *H. seligeri* and for the occurrence of all forest-interior species (see above) but *N. curvifolia*. Predictive models were also built for many of the comparison species both concerning occurrence and abundance.

The study showed that forest-interior species can inhabit early-successional forests arisen after logging. However, it was concluded that all CWD in young stands immediately surrounding woodland key habitats should be excluded from biofuel harvest because species specific guidelines are not useful for the forest industry.

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Introduction

After the rise of modern forestry in the 1950s with the use of clear-cuts (Fries and Lämås 2000), Swedish managed forests have seen a decrease in the amount of coarse dead wood (Linder & Östlund 1992) and the reduction of dead and dying trees is now thought to be the biggest threat to flora and fauna in boreal forests (Siitonen 2001). In fact, 50% of all red-listed species in Sweden are dependent on dead wood for their survival (Gärdenfors 2005). Furthermore the increasing demand for logging residues for energy production risk decreasing the dead wood amounts in managed forests even more. It is therefore important to investigate the effect of the residue harvest, especially the types effecting coarse woody debris (>10 cm diameter, CWD hereafter).

Old growth, natural, boreal forests have typically more CWD than managed forests (Siitonen et al. 2000). In Sweden the setting aside of woodland key habitats have proved to be a way of maintaining areas with substantially more CWD than the surrounding forest within the production forest landscape. Woodland key habitats are areas in the managed forests that the Swedish forest agency has recognised as extra valuable in terms of hosting red-listed species or to be very likely to host red-listed species and are now commonly set aside in the Swedish forestry (Hansson 2001). They often have many structures typical of forests with a long continuity of tree coverage, like logs and snags (Jonsson and Jonsson 2007). They are meant to act like species rich islands and sources of dispersal in the production forest landscape (Anonymous 2005). However, they only cover about 1% of the production forest landscape in Sweden (Anonymous 1997 and Anonymous 2002) making these sources of dispersal very fragmented.

The value of dead wood for living organisms, especially logging residues after a clear cut, in young managed boreal forests is not clear. Some work has been done to imitate CWD substrates of natural forests in managed forests. High stumps are considered very valuable for conservation efforts in managed forests (Jonsell et al. 2004, Jonsell and Weslien 2003, Lindhe and Lindelöw 2004). It is now a common practise to leave high stumps on clear cuts for conservation purposes (Anonymous 1993). High stumps are even created if natural ones are not present. However, the knowledge about the conservation impact and importance of low stumps and other CWD objects created by logging as substrates for epixylic organisms in young managed forests is still limited (but see Caruso et al. 2008, Kantvilas and Jarman 2006 and Humphrey et al. 2002). After logging, stumps form the bulk (~24 m^3/ha) of dead wood volume with about ten times the volume of fine woody debris (<10 cm diameter, hereafter FWD) on clear-cuts (Caruso et al. 2008) making them potentially important for dead wood inhabiting organisms in boreal production forests.

There is an increasing demand for logging residues for bioenergy, and FWD is already extracted from clear-cuts. This extraction will most likely continue to increase (Lundborg 1998) and there is also a potential for an increase in the harvest of stumps created at final felling (Berglund 2006; Hofsten 2006). Although a large out-take of these logging residues will probably not harm biodiversity if done in an ecologically proper manner - in fact there are reports suggesting that it can contribute to a good environment (Lundborg 1998) - caution must be taken not to remove dead wood that could benefit biodiversity, e.g. stumps with rare species (Nascimbene et al. 2008). In a landscape with only very fragmented clusters of dead wood a large scale stump harvest simply risk reducing the diversity of epixylic species if it is not conducted in a manner that ensures maximum benefit for biodiversity, i.e. leaving the most valuable stumps. However, it is worth remembering that logging with the use of clear cuts also has made epixylic, open-forest species (i.e. species with early-successional forests as their primary habitat) common by creating dead wood in sunny positions. While there might

not be an immediate risk of these species becoming red-listed, removing their substrates would probably decrease their population sizes.

Stumps have measurable qualities that are connected to the diversity of lichens and bryophytes (Caruso and Rudolphi 2009). It can be assume that the same is true for all dead wood. Therefore it is possible to create predictive models based on a number of relevant variables to determine where the dead wood valuable for epixylic, forest-interior species (i.e. species that are considered to be confined to boreal forests in late-successional stages) in young production forests might be and what qualities it has.

Generally, forest-interior species are not considered to survive the clear cut phase in the succession of a production forest due to their sensitivity to altered microclimate (Hannerz and Hånell 1997, Fenton et al. 2003 and Hylander et al. 2005). However, young stands bordering woodland key habitats are interesting because they are close to a source of propagules and are likely to have a more favourable microclimate than young stands that do not border a woodland key habitat. Most dead wood objects in a young stand probably do not act as substrates for forest-interior species. Therefore it is vital to know which qualities are important for saving those specific dead wood objects.

Among lichens and bryophytes there are many epixylic species. Because they are visible most of the year, as long as there is no snow cover, they make excellent study organisms for the importance of CWD in young stands. Both lichens and bryophytes react fast to changes in their environment, lichens because they consist of two or more organisms and bryophytes because they lack the water transporting capability of vascular plants. Boreal forests are also generally poor in vascular plats but potentially rich in lichens and bryophyte species (Nitare 2000).

The aim of this study was to investigate whether forest-interior species in fact can inhabit early-successional forests arisen after logging. This was done by analysing the effects of local environmental variables, propagule sources, and distance to a bordering woodland key habitat on the presence and abundance of a forest-interior epixylic bryophyte, *Anastrophyllum hellerianum*, in young managed forest stands. I did the same analyses for other forest-interior bryophytes, and for comparison I also included epixylic bryophytes and lichens considered open-forest species and generalist species (species with no preference for either forest-interior or open-forest).

Material and Methods

Landscape

The study was conducted in five sites in the northern part of the county of Uppland (figure 1), Sweden. This is southern boreal forest bordering to hemiboreal forest. The macro vegetation is dominated by Norway spruce *Picea abies* Karst. and Scots pine *Pinus sylvestris* L. Modern silviculture with clear-cuts dominates the use of the forest landscape so that the forest stands are even-aged and, to a large extent, homogenous in tree species composition.

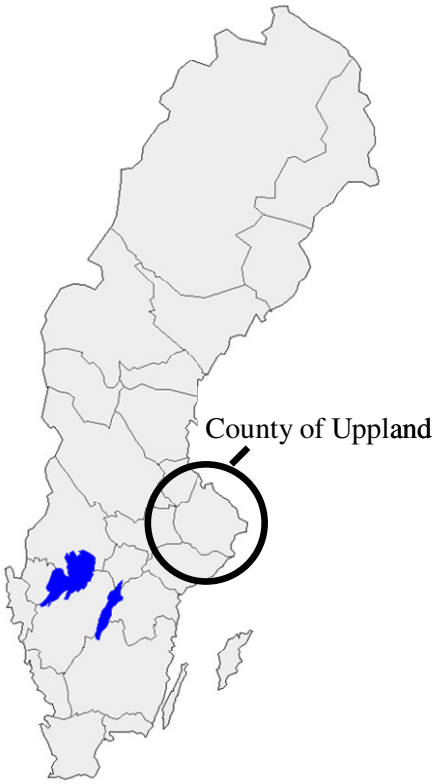

Figure 1. *Map of Sweden with the county of Uppland indicated with a cirkle*

Study sites

Each site consisted of two adjoining stands as shown in figure 2: one late-successional woodland key habitat (98-146 years old) with presence of *Anastrophyllum hellerianum*, and one early-successional young stand, clear-cut 6-16 years ago. No consideration was taken to when the stands were planted. The border between the woodland key habitat and the young stand was straight for at least 100 metres.

The GIS (Global Information System) software ArcGIS 9 was used to locate possible study sites from data obtained from the forestry companies Holmen Skog, Bergvik and Sveaskog. These sites were then inspected to fill the requirements necessary for the study.

To make sure the woodland key habitat of each site was the closest and thus the most likely propagule source of *A. hellerianum* and other forest-interior species for the CWD objects of the young stand, other stands older than 90 years surrounding the young forests had to be at least 50 metres away from the inventoried plot. See table 1 for a list of the study sites.

Table 1. Names and coordinates of the five study sites

Name	Coordinates
Holmen 6239	59° 54,88′ N 18° 1,34′ E
Holmen 1966	59° 52,92′ N 17° 53,08′ E
Holmen 4731	59° 54,36′ N 18° 0,34′ E
Bergvik 9595	60° 7,68′ N 16° 47,48′ E
Bergvik 8232	60° 17,34′ N 17° 15,45′ E

Plots

On the 100 metre straight border to the woodland key habitat a 50x50 metres plot was indicated in the young stands. The plot was divided in eight subplots parallel to the border, each subplots being 6.25x50 metres.

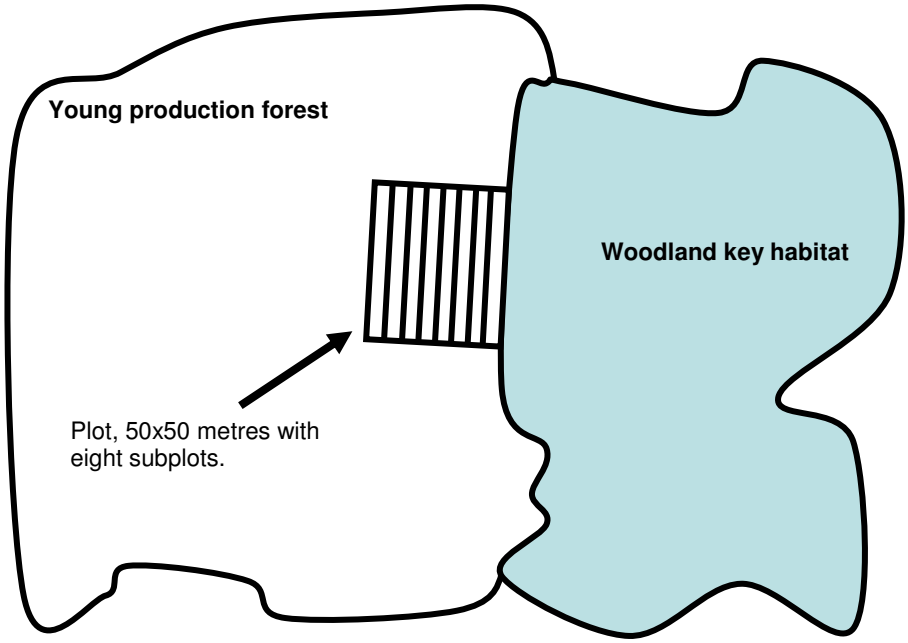

Figure 2. *Schematic view of an exemplified study site.*

Study species

Study species were chosen to represent both common and less common species. Both bryophyte and lichens species classified, by species experts (T Hallingbäck for bryophytes and G Thor for lichens), as forest-interior species, generalist species and open-forest species were included. Species that are difficult to classify in the field were not included. The number of species was limited to ten by practical reasons of the study. The lichen nomenclature follows Santesson et al. (2004) and the bryophyte nomenclature follows Hallingbäck et al. (2006). The vascular plant nomenclature follows Krok and Almquist (2004). The following ten species were included in the inventory:

- Forest-interior species

Anastrophyllum hellerianum is a small, boreal, red-listed (NT), epixylic hepatic with up to 1cm high shoots (Söderström, 1984). It is also an indicator species in the Swedish forest agency's system of indicator species ("signal species"), indicating long continuity of logs in different stages of decay (Nitare, 2000). Characteristic for the species are the red asexual diaspores in the top of the shoots making it easily recognizable. The asexual diaspores are also the main means of dispersal, as sexual diaspores are less common, making it mainly a short distance disperser (Pohjamo *et al.*, 2006). It is usually reported on logs of *P. abies*, *P. sylvestris* and sometimes *Populus tremula* (Söderström, 1984).

Buxbaumia viridis is a small, southern, epixylic moss that is used as an indicator species, in the Swedish forest agency's system of indicator species ("signal species"), indicating long continuity of CWD in different stages of decay and high, relative air humidity. It mostly grows on CWD from *P. abies* but sometimes also from *P. sylvestris* and leafy tree species. The main feature that makes it easily recognizable is the big sporophytes that grow up to 7 mm (Nitare, 2000). The rest of the moss is very inconspicuous (pers. comm.). It is protected from plundering in Sweden (The Swedish government, 2007).

Herzogiella seligeri is a southern, epixylic moss that is used as an indicator species in its northern range, in the Swedish forest agency's system of indicator species, indicating long continuity of most types of CWD in different stages of decay and high, relative air humidity. The characteristic sporophytes are almost always present (Nitare, 2000).

Lophocolea heterophylla is the most common epixylic hepatic in southern Sweden and is to be found all over the country except in the mountains of the northwest. It grows on all kinds of CWD. The species epithet refers to the two kinds of differently shaped leaves (Hallingbäck *et al.*, 2008).

Nowellia curvifolia is an epixylic hepatic that is used as an indicator species in its northern range in Sweden, in the Swedish forest agency's system of indicator species ("signal species"), indicating long continuity of CWD in different stages of decay and high, relative air humidity. It mainly grows on logs of *P. abies* and *P. sylvestris* in late stages of decay. The characteristic, elongated shoots are usually not branched and have a reddish colour (Nitare, 2000).

- Generalist species

Calicium glaucellum is an epixylic pin lichen that is fairly common throughout Sweden. It mainly grows on coniferous CWD (Hallingbäck, 2010) and can appear in great quantity on snags, but also on stumps, logs (pers. obs.) and slash (Caruso *et al.*, 2008).

Calicium trabinellum is an epixylic pin lichen that grows on coniferous CWD, mainly on snags. It has, in Sweden, its main range north of *limes norlandicus* (Hallingbäck, 2010).

Xylographa parallela is an epixylic lichen that grows on CWD in open and dry positions, mostly on logs (Hallingbäck, 2010). The apothecia are sunk into the surface of the wood as elongated dark markings, making it look like someone has drawn with a pen on the wood. The colour of the apothecia can vary from reddish to brown (pers. comm.).

- Open-forest species

Cladonia botrytes is an epixylic lichen that has been greatly favoured by modern silviculture in that it grows frequently on coniferous stumps in later stages of decay in sunny positions (pers. obs.). Coniferous logs are also occupied. Occurrence on non coniferous substrates is uncommon in Sweden (Hallingbäck, 2010). The up to 2cm high podetia, that almost always have lots of beige apothecia, makes this species easy to recognize (pers. comm.).

Mycocalicium subtile is a non lichenized, epixylic fungus (Keller *et al.*, 2007) that is very common on snags, mainly coniferous, and other dry CWD in open positions (Jüriado *et al.*,

2004). It has the appearance of a pin lichen which stains the wood whitish and has black thin fruiting bodies (pers. comm.).

Data collecting

- Species registration

The inventory was performed in the autumn of 2009.

In the 50x50 m plot in the young stand every CVD object were searched for the study species. Snags were only searched up to two metres above ground level. Furthermore the five first FWD objects in each subplot were searched to include the possibility that the FWD may in fact act as substrates as well. The minimum size for FWD was 1 cm in diameter and 1 m in length. The subplots acted as a measure of distance to the bordering woodland key habitat, i.e. distance 1-8.

There were no time restrictions on the inventory of the young forests.

Abundance (cm^2) of the species was measured.

- Explanatory variables

The CWD/FWD objects in the young stands were classified to species (even in difficult cases the dead wood objects were classified to species based on the present physical characteristics), degree of decomposition, degree of shadowing and type of CWD/FWD object, i.e. stump, log or snag (branches were treated as logs in the subsequent statistical analysis). Snags that were too high to practically be measured were instead estimated visually to height.

To estimate the degree of decomposition a knife was pushed into the dead wood objects from the side. A modification of the method described in Hottola and Siitonen 2008 was used with decomposition estimates 1-5, see table 2. Because a single object could contain several parts with different degrees of decomposition the estimate was taken in four different directions so that a mean for each object could be calculated.

Table 2. The different degrees of decomposition in the dead wood objects measured with a knife.

1	The wood is hard. The knife penetrates only a few mm.
2	The wood is slightly decayed. The knife penetrates 1-2 cm.
3	The wood is moderately decayed. The knife penetrates 2-5 cm.
4	Most of the wood is soft throughout. The entire blade penetrates.
5	The wood is very soft. It disintegrates when lifted.

The degree of shadowing was estimated from a scale of 1-3, where 1 was no shadowing, 2 was partial shadowing and 3 was complete shadowing.

To calculate the volume of dead wood in the young stands the five first FWD objects in every subplot and all CWD objects was measured for diameter and height/length. The diameter was measured at the middle of the object (diameter for snags were measured 1.5 metres above ground level). The formula for a cylinder was used to calculate volume.

When calculating the area of the dead wood objects 25 % of the area was taken of the logs since a majority of them lay against the ground making it impossible for bryophytes and lichens to grow on the parts facing the soil.

To test for effects of metapopulation size I used the variables occupancy (= the proportion of dead wood objects occupied by a species) and abundance (= total cover of a species) in the young forests.

In the woodland key habitats I set a time of two hours to search for the study species, listed above, on CWD objects. As in the young stands, snags were only searched up to two metres above ground level. I started at one end of the border to the young stand and moved away from the border in a sinus shape into the woodland key habitat (Fig. 3). There was no distance limit to the border of the young production forest. In the event of a hit the species in question was recorded concerning abundance (cm^2). In this way I standardized the inventory in the woodland key habitat by time instead of plot size. It has the advantage of not risking that a set study plot ends up in a space, by chance, where there is no CWD. Opposite to a young production forest that has recently been clear cut, and thus is full of harvest stumps, the CWD in a woodland key habitat cannot be assumed to be spread out evenly, but rather to show a more random pattern to where the trees have happened to fall down (pers. obs.). In this way I got a relative figure of the population of each species in the woodland key habitat, a measurement of cover/time unit and a measurement of presence/time unit, which represented the true population better than a single, randomly placed plot, would have done. I then used presence and abundance of the study species, respectively, in the woodland key habitats as a variable to test for propagule source.

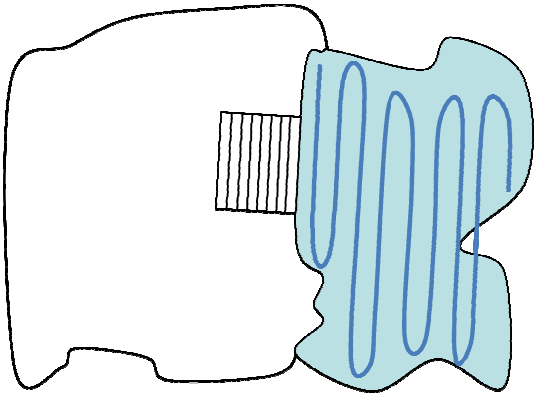

Figure 3. Indicated in blue is the pattern I moved after in the woodland key habitat.

Statistical analysis

To test for effects of explanatory variables on occurrence probability and abundance of individual bryophyte and lichen species on a specific dead wood object in the young stand, I built generalized linear regression models. This was done in the statistical software SAS 9.2. By setting "stand" as a random factor I accounted for the non-independence of dead wood objects within stands. For occurrence probability I assumed binomial distributions, and used a logit link function (logistic regression). For each species, one binary response variable was occurrence (1) or no occurrence (0) in a dead wood object. The abundance data was logged with a base of ten to be normally distributed.

In building the models I used variable reduction on several levels.

First I fitted every variable (table 3) singly and only saved the ones with a p-value < 0.2.

The second level was done differently for the models explaining presence and abundance. For the models explaining abundance the remaining variables were all fitted into the model after which I took out the variable with the highest p-value one by one until the lowest AIC number (pseudo-likelihood) for the model was achieved. These variables were then considered to constitute the model of explanatory factors for abundance of that species.

Because SAS 9.2 log regr. does not give AIC-values only p-values were used for the presence-models. After the remaining variables were fitted into the models explaining presence I removed the variable with the highest p-value one by one until all remaining variables had a p-value < 0.1. The remaining variables were then considered to constitute the model of explanatory factors for presence of that species.

I also checked for correlations between the explanatory variables. No correlations were found.

Table 3. The variables that were fitted in the models

	Stand variables
1	Occurrence in young forest.
2	Occurrence in woodland key habitat.
3	Abundance in young forest.
4	Abundance in woodland key habitat.
5	Volume of dead wood in the young forest study plot.
	Dead wood object variables
6	Area.
7	Degree of decomposition of the dead wood object.
8	Degree of shadowing.
9	Bark coverage.
10	Species.
11	Type (stump/log/snag).
12	Distance to the border of the woodland key habitat.

Results

In total 758 dead wood objects were searched in the young stands out of which 556 were CWD and 202 were FWD. They consisted of 442 stumps, 223 logs, 8 snags and 85 branches.

Table 4. Total number of occupied dead wood objects and occupied stands in the young stands and woodland key habitats (W.k.h) respectively. In total there were five study stands.
F-i = Forest interior, G = Generalists, O-f = Open forest

		Young stand			W. k.h.
Habitat preference	**Species**	**No. occupied CWD objects**	**No. occupied FWD objects**	**No. occupied stands**	**No. occupied stands**
F-i	*Anastrophyllum hellerianum*	15	1	4	5
F-i	*Buxbaumia viridis*	15	-	1	2
F-i	*Herzogiella seligeri*	11	-	4	3
F-i	*Lophocolea heterophylla*	88	15	5	5
F-i	*Nowellia curvifolia*	-	-	-	2
G	*Calicium glaucellum*	34	-	5	-
G	*Calicium trabinellum*	1	-	1	-
G	*Xylographa parallela*	118	44	5	2
O-f	*Cladonia botrytes*	156	12	5	1
O-f	*Mycocalicium subtile*	91	7	5	4

The occurrence models

Models explaining occurrence were fitted for *Anastrophyllum hellerianum, Buxbaumia viridis, Herzogiella seligeri, Lophocolea heterophylla, Calicium glaucellum, Xylographa parallela, Cladonia botrytes,* and *Mycocalicium subtile* (table 5). But not for *Nowella curvifolia* and *Calicium trabinellum* for which there were insufficient data.

- Forest-interior species

Decreasing distance to the woodland key habitat increased the occurrence of *Anastrophyllum hellerianum* and *Lophocolea heterophylla* in the young stands. Increasing bark cover decreased the occurrence probability of the former and increased the occurrence probability of the latter.
In addition, the occurrence of *L. heterophylla* was positively affected by increasing occupancy in the young forest, increasing area of dead wood object, increasing shadowing and increasing decomposition. Finally, increasing decay also increased the occurrence of *Buxbaumia viridis* and *Heterophylla seligeri*.

- Generalist species

Increasing area of the dead wood objects increased the occurrence of *Calicium glaucellum* and *Xylographa parallela*. Increasing decomposition also positively affected the occurrence of *C. glaucellum*. The occurrence of *X. parallela* was positively affected by increasing occupancy in the young stands, increasing distance to the borders of neighbouring woodland key habitats, if the dead wood objects were *Picea abies* or *Pinus sylvestris* and with decreasing bark cover.

➢ Open-forest species

Increasing distance to the borders of neighbouring woodland key habitats, if the dead wood objects were a stump or a log and increasing area of the dead wood objects increased the occurrence probability of *Cladonia botrytes* and *Mycocalicium subtile*. Increasing occupancy in the same young stand, if the dead wood objects were *Picea abies* or *Pinus sylvestris*, increasing decomposition and decreasing shadowing positively affected the occurrence of *C. botrytes*. Also, decreasing bark cover positively affected the occurrence of *M. subtile*.

Table 5. Models containing variables with p-values < 0.1 explaining occurrence of the species in young stands. F-i = Forest interior, G = Generalists, O-f = Open forest, w.k.h. = Woodland key habitat, y.f. = Yong forest

Habitat preference	Species	Variables	Estimate	Standard error	Pr > F
F-i	***Anastrophyllum hellerianum***	Distance to border of w.k.h.	-0.28	0.13	0.04
		Bark cover	-0.04	0.02	0.02
F-i	***Buxbaumia viridis***	Decomposition	0.83	0.32	0.94E-2
F-i	***Herzogiella seligeri***	Decomposition	0.64	0.29	0.03
F-i	***Lophocolea heterophylla***	Occurrence in y.f.	0.06	0.01	0.04
		Distance to border of w.k.h.	-0.31	0.06	<0.10E-3
		Area of dead wood object	0.24E-4	8.03E-6	0.35E-2
		Decomposition	0.31	0.11	0.36E-2
		Shadowing	0.50	0.27	0.07
		Bark cover	0.75E-2	0.42E-2	0.07
G	***Calicium glaucellum***	Area of dead wood object	0.47E-4	9.59E-6	<0.10E-3
		Decomposition	0.45	0.18	0.01
G	***Xylographa parallela***	Occurrence in y.f.	0.02	0.80E-2	0.09
		Distance to border of w.k.h.	0.09	0.04	0.04
		Species of dead wood object			
		P. abies	2.49	0.92	<0.10E-3
		P. sylvestris	1.27	0.95	
		Leafy tree species	0	-	
		Area of dead wood object	0.48E-4	9.79E-6	<0.10E-3
		Bark cover	-0.02	0.43E-2	<0.10E-3
O-f	***Cladonia botrytes***	Occurrence in y.f.	0.03	0.01	0.08
		Distance to border of w.k.h.	0.16	0.04	0.20E-3
		Species of dead wood object			
		P. abies	1.97	1.04	0.12E-2
		P. sylvestris	2.71	1.04	
		Leafy tree species	0	-	
		Type of dead wood object			
		Stumps	2.60	0.74	<0.10E-3
		Logs	1.89	0.77	
		Standing dead wood >2 metres in height	0	-	
		Area of dead wood object	0.03E-3	9.07E-6	0.11E-2
		Decomposition	0.17	0.10	0.09
		Shadowing	-0.38	0.20	0.05
O-f	***Mycocalicium subtile***	Distance to border of w.k.h.	0.10	0.05	0.08
		Type of dead wood object			
		Stumps	2.52	0.75	<0.10E-3
		Logs	0.75	0.79	
		Standing dead wood >2 metres in height	0	-	
		Area of dead wood object	0.47E-4	9.78E-6	<0.10E-3
		Bark cover	-0.02	0.53E-2	0.20E-3

The abundance models

Only *Anastrophyllum hellerianum, Herzogiella seligeri, Calicium glaucellum* and *Mycocalicium subtile* had normally distributed abundances in the young production forests after the data was log-transformed with a base of ten, hence models explaining abundance were fitted only for these species (table 6).

- Forest-interior species

Decreasing decomposition and shadowing increased the abundance of *Anastrophyllum hellerianum*, while dead wood objects of *Picea abies* material decreased the abundance of the same.

Increasing occupancy in the young forest increased the abundance of *Herzogiella seligeri*.

- Generalist species

Decreasing decomposition and increasing area of the dead wood objects increased the abundance of *Calicium glaucellum*.

- Open-forest species

Increasing area of the dead wood objects, if the objects were *Picea abies* or *Pinus sylvestris* and decreasing bark cover increased the abundance of *Mycocalicium subtile*.

Table 6. Models containing variables with p-values < 0.1 explaining abundance of the species in young managed forests.
F-i = Forest interior, G = Generalists, O-f = Open forest, y.f. = Yong forest

Habitat preference	Species	Variables	Estimate	Standard error	Pr > F	AIC
F-i	***Anastrophyllum hellerianum***	Species of dead wood object				
		P. abies	-0.55	0.46	0.27	27.34
		P. sylvestris	0	-		
		Leafy tree species	-	-		
		Decomposition	-0.33	0.19	0.13	
		Shadowing	-1.12	0.41	0.022	
F-i	***Herzogiella seligeri***	Occurrence in y.f.	0.13	0.050	0.040	14.88
G	***Calicium glaucellum***	Decomposition	-0.17	0.099	0.088	89.06
		Area of dead wood object	8.65E-6	3.75E-6	0.029	
O-f	***Mycocalicium subtile***	Area of dead wood object	0.000014	4.25E-6	0.0017	201.31
		Type of dead wood object				
		Stumps	0.98	0.44	0.074	
		Logs	0.81	0.46		
		Standing dead wood >2 metres in height	-	-		
		Bark cover	-0.0084	0.0033	0.012	

Discussion

Forest-interior species occur in young managed stands

This study shows that epixylic species that are considered to be confined to boreal forests in late-successional stages (i.e. forest-interior species), like *Anastrophyllum hellerianum*, in fact can inhabit CWD in early-successional forests arisen after logging. In this way they create a population fringe close to a woodland key habitat. Indeed other forest interior species like *Lophocolea heterophylla* was very common and *Herzogiella seligeri* was found in more young stands than woodland key habitats (table 4). One reason for why they have possibly been overlooked in the young stands is that clear cuts have been associated with problems concerning nature conservation rather than something that can be positive. In other words, clear cuts have been regarded as unsuitable for forest-interior species. Another reason might be that studies have looked at young stands in general rather than young stands bordering old growth forest (but see e.g. Hylander 2009). This shed new light on the importance to learn more about where epixylic forest interior species inhabit CWD in young stands created by logging, especially red-listed ones.

If the CWD in young stands bordering old growth forests were to be removed indiscriminately the population fringe close to the old growth forest would disappear. We do not know how this population fringe contributes to propagule spreading, but several studies suggest that remnants of old growth forest act as propagule sources in the boreal production forest landscape (e.g. Vanha-Majamaa and Jalonen 2001, Fenton and Frego 2005). However, not all forest-interior species are likely to produce propagules in young stands due to stress caused by increased light conditions, lower humidity etc (Hylander 2005). Hylander (2009) found that only ~50% of forest-interior bryophyte species in young stands produced spores. But on the other hand that is not something that this study has shown specifically. On the contrary both *A. hellerianum* and *Buxbaumia viridis* were recognised by their propagule bodies (*A. hellerianum* by gemmae and *B. viridis* by sporophytes). As these organisms are dependent on patchy substrates scattered in the landscape, the size of propagule source is likely to have a substantial effect on the species capability to colonize new substrates. Sundberg et al. (2006) showed that size of propagule source (i.e. a population that produces propagules) matters, in a study of *Sphagnum* spp. A very common species ~40 km away on the mainland colonized an island better than species on neighbouring islands. But it also showed that a smaller, local spore source (i.e. a population closer to the island) dominated the spore rain up to 200 m from its location. In other words a propagule source increases its distance of spreading with size (i.e. population size), but also has a local range of dominance regardless of size (i.e. a small propagule source has a range where its propagules dominates even though there is a substantially bigger population further away). Considering the small portion and scattered locations of the woodland key habitats in the production forest landscape, fringes around these populations are not of irrelevance but rather a large proportion of the population sizes and thus may influence capability of spreading.

Restricted dispersal or microclimatic gradients?

Previous studies suggest that lichens are strongly dispersal limited (e.g. Sillet et al. 2000, Dettki et al. 2000, Hilmo & Sistad 2001), even though Johansson & Ehrlen (2003) suggest that occupancy patterns are difficult to explain with dispersal mechanisms alone. For bryophytes, studies are contradicting each other on whether they are dispersal limited (Snäll et

al. 2003, Kimmerer 2005, Pharo and Zartman 2007) or not (Bremer and Ott 1990, Miller and McDaniel 2004, Munoz et al. 2004, Hutsemekers et al. 2008). Probably it is dependent on if sexual or asexual propagules are used when it comes to bryophytes (Murrell et al. 2002) but also on the size of propagules (Pohjamo et al. 2006). Because my study plots reached only 50 metres from the borders of the woodland key habitats and no lichens in the study were classified as forest-interior species it is reasonable to think that the only forest-interior species limited by dispersal would be bryophytes with an inclination towards asexual reproduction. Indeed, the occurrence probability of two forest-interior bryophytes (*Anastrophyllum hellerianum*, *Lophocolea heterophylla)* increased with decreasing distance to the border of the woodland key habitats, whereas the occurrence of one generalist (*Xylographa parallela)*, and two open-forest *(Cladonia botrytes* and *Mycocalicium subtile)* lichens increased with increasing distance to the border. This also point towards *X. parallela* being more of an open-forest species than a generalist species. However, it is likely that none of these species are dispersal limited on this scale. The pattern is probably due to the gradient of e.g. microclimate with distance to the border of the woodland key habitat. Indeed there are studies suggesting that asexual diaspores of *A. hellerianum* also travel on a landscape level (Pohjamo et al. 2006). There is also a possibility that the distance dependence for these two bryophytes is affected by both a gradient in micro climate and dispersal limitation. Even though Pohjamo et al. (2006) suggest that a substantial part of the asexual diaspores of *A. hellerianum* travel longer distances, most of the diaspores spread within a few metres from the source.

Importance of dead wood quality

It is also clear from this study that different epixylic species benefit from different qualities of the dead wood. This is in line with previous research suggesting a succession of species communities over time as the wood deteriorates (e.g. Caruso and Rudolphi 2009).

If high shadowing is something that would positively affect forest-interior species, it follows this pattern for the occurrence of *Lophocolea heterophylla* and in revers it was negative for the occurrence of *Cladonia botrytes* (Open-forest). However, the abundance of *Anastrophyllum hellerianum* was also positively affected by decreasing shadowing.

Bark cover was interesting in that only one species benefitted from high coverage, *L. heterophylla*, and indeed it is often found behind loose bark on stumps and logs (pers. obs.).

All the generalist and open-forest species were positively affected, concerning occurrence as well as abundance, by the area of the dead wood objects. Only the occurrence of one forest-interior species was affected (positively) by the area, *L. heterophylla*. This might point towards a bigger background rain of propagules of the generalist and open-forest species in the young stands and that the forest-interior species are more limited by variables concerning micro climate. It might also point towards that *L. heterophylla* is more of a generalist species than a forest-interior species.

Local impact of metapopulation size

Because epixylic species inhabit patchily distributed, temporal substrates they are expected to demonstrate features typical for metapopulations (e.g. Söderström & Herben 1997). Therefore it is interesting that the abundance of the forest interior species *Herzogiella seligeri* and the occurrence of one species from each habitat preference were positively affected by increasing occupancy of the same species in the young forest. In other words, the bigger the metapopulation of *Lophocolea heterophylla*, *Xylographa parallela* and *Cladonia botrytes* the

higher probability of these species occupying a CWD substrate and the higher abundance of *H. seligeri* on a given substrate. One reason for why these species show this pattern and not all the study species might be that these species are better equipped to spread within the open habitat of a young forest. This might also indicate that *L. heterophylla* is more of a generalist species than a forest-interior species. However, the result of this is inconclusive as half of the generalist and open-forest species did not show this pattern.

Suggestions for further research

Aspect is widely used as a variable on landscape level (Chen et al. 1993, 1995) and has been shown to have a big impact on lichens and bryophytes (Hazell & Gustafsson 1999 and Kivistö & Kuusinen 2000). However, as shown in Kivistö & Kuusinen (2000) aspect is related to differences in micro climate. Therefore aspect is very useful on a landscape level, but is not taken into consideration in this study due to the local focus on the individual dead wood objects. Future studies should clarify if aspect affects forest-interior species in young stands bordering woodland key habitats.

It is useful, but also difficult to know on what level a species is dispersal limited. Tools are needed to distinguish between dispersal limitations on a local level and variable gradients on the same.

I did not differ between CWD and FWD in the statistical analysis. This poses the question if CWD and FWD are equally important in young stands or if one is more important than the other. Caruso et al. (2008) compared the species diversity on slash and stumps in young boreal stands in Sweden and found that the majority of species found on both substrates were more frequent on stumps, which also had a higher number of unique species and species in the literature indicated as nationally rare or uncommon. Furthermore they stated that few epixylic lichen species were strictly associated with slash, whereas stumps may provide important habitats for rare lichens in the managed forest landscape. They got this result even though only the cut surfaces of the stumps were searched. Because I searched both cut surfaces and sides of all FWD and CWD it is reasonable to think that their result was even more pronounced in my study. However, because my young stands were all neighboring woodland key habitat there is a possibility that the FWD play a more important role there for biodiversity than in young stands generally. E.g. the forest-interior species *Anastrophyllum hellerianum* and *Lophocolea heterophylla* was found on one and fifteen FWD objects respectively in the young stands. Future research should address this question.

Conclusions

It is possible to say that dead wood is valuable as substrates for the study species in a young stand bordering a woodland key habitat. This is important because it gives us a tool to discriminate between CWD valuable for energy harvest and CWD valuable for biodiversity. However, similar and bigger studies need to be conducted to map the extent of biodiversity, especially red-listed species in young stands surrounding old growth forest and to what locations these qualities are bound.

The qualities of CWD as a result of logging are uniform at the time of harvest. A fresh harvest stump will for example not be suitable for a species that need slightly decayed CWD. If the guideline for that species is to save the CWD of a certain degree of decay all stumps will be taken and there will be nothing left to decompose to the right level. Therefore guidelines connected to location are more useful than substrate variables for the industry. At this point the guidelines, based on this study, for biofuel harvest should be to exclude all harvest of CWD from young stands immediately surrounding woodland key habitats.

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