All scales matter
– effects on the landscape-, stand-, substrate- and temporal scale on occurrence of two dead-wood living microlichens

Alla skalor spelar roll – effekter av landskap, ståndort, substrat och tid på två vedlevande mikrolavar

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Abstract

All scales matter – effects on the landscape-, stand-, substrate- and temporal scale on occurrence of two deadwood living microlichens
Edith Bremer

Understanding extinction debt and how species are affected by landscape structure is important knowledge in order to form strategies for species protection in forestry and conservation. In this study, I investigate whether an extinction debt can be detected in two deadwood living lichen species by modelling their occurrence against past and present habitat amount in the landscape as well as amount of continuity forest (i.e. forests that never have been clearcut). A second objective was to assess the importance of landscape-scale characteristics compared to stand- and substrate characteristics for the occurrence of these species. I surveyed 55 stands in northern Sweden for occurrence of *Hertelidea botryosa* and *Cladonia parasitica*, as well as amount and characteristics of their deadwood substrate. From my results, I could neither confirm nor refute extinction debt in either species based on any landscape level effects. The species were decidedly more dependent on substrate characteristics, but also stand and landscape characteristics were important. The high dependency of these species on specific types of deadwood that are not easily recreated in a managed landscape indicates that the habitat amount in the landscape might be of greater importance than could be shown here as areas were classified as possible habitat based only on information about forest age and continuity without knowledge on the availability of the specific type of deadwood substrate. As the type of deadwood substrate preferred by the species is only created in specific stands and landscapes, and takes considerable amounts of time to produce, my results still underlines the importance for efforts in forest management to secure continuous supply of these deadwood qualities and to protect areas were such deadwood already exists.

Keywords: extinction debt, deadwood, microlichens, continuity forest, landscape structure

Populärvetenskaplig sammanfattning

Inom ekologin är det etablerad kunskap att en arts fortlevnad inte bara påverkas av dess växtplats. Det är också viktigt hur mycket potentiell växtplats, så kallat habitat, som finns i landskapet runtomkring. Eftersom den naturliga miljön är i konstant förändring så växlar det ständigt vilka områden som är lämpligt habitat för en art. Om livsmiljön försämras på en plats behöver det finnas nytt habitat tillgängligt som arten kan sprida sig till.

Om mängden habitat i landskapet skulle minska, kan arter ibland ändå leva kvar i små fickor med bevarat habitat. Men över tid riskerar arten ändå att dö ut när den blir isolerad och inte kan sprida sig till nya platser. Detta kallas för en utdöendeskuld. Kunskap om utdöendeskulder och om landskapets inverkan på arters överlevnad är viktigt för naturvården eftersom det påverkar hur arter klarar att överleva i ett område över tid.

Idag finns över 300 rödlistade arter i Norden som är beroende av död ved för sin överlevnad. Deras habitat utgörs ofta av gamla skogar med lång kontinuitet, dvs skog har funnits där kontinuerligt utan att någonsin kalavverkas av människor. Där finns gott om död ved i olika nedbrytningsstadier som skapas när träden får växa sig stora och gamla för att sedan dö och förmultna på plats. Arter knutna till dessa träd har svårt att överleva i det hårt brukade skogslandskap som kommit att dominera i Norden sedan förra seklet. Det mesta av Sveriges kontinuitetsskogar har omvandlats till produktionsskog och arter knutna till skogarna har minskat kraftigt.

I den här studien har jag undersökt om det finns en utdöendeskuld för vedskivlav (*Hertelidea botryosa*) och dvärgbägarlav (*Cladonia parasitica*) i norra Sverige. Båda arterna är rödlistade och lever bara på död ved. Jag undersökte också om det var vedens, skogens eller landskapets egenskaper som var viktigast för att lavarna skulle växa på en plats. Jag besökte 55 nyckelbiotoper och naturreservat från östra Jämtland till centrala Norrbotten. Där mätte jag mängden död ved och den döda vedens egenskaper. Jag räknade hur många döda träd jag hittade med någon av lavarna. För att undersöka landskapets betydelse använde jag mig av tillgängliga data från Naturvårdsverket om mängden skog i landskapet med kontinuitet. För att undersöka om det fanns en utdöendeskuld för lavarna behövde jag kunna jämföra om lavarna påverkades mest av historisk eller nutida habitatmängd. Jag använde flygbilder från 2019 och 1960 och undersökte mängden habitat i landskapet vid respektive tillfälle.

Det som bäst förklarade båda arters förekomst var den döda vedens egenskaper. Stor diameter, sent nedbrytningsstadie, ved som kolats genom gamla skogsbränder och att veden inte är täckt av mossa eller bark, är alla viktiga egenskaper som gynnar vedskivlav och dvärgbägarlav. De föredrog att växa på liggande döda träd hellre än stående. Eftersom jag bara inventerade i gammal skog visade det sig att variationen i tillgången på död ved mellan platserna var för liten för att man skulle kunna se någon trend av volymen död ved i skogen runtomkring. På landskapsnivå gynnades vedskivlav av kontinuitetsskog. Dvärgbägarlav gynnades av mängden nutida habitat. Inget av det här är bevis för en utdöendeskuld.

Som slutsats kan sägas att det viktigaste för vedskivlav och dvärgbägarlav är att det finns död ved av rätt kvalitet. Det är alltså den minsta skalan i form av lavarnas växtplats som är av störst vikt. Den omkringliggande skogen och landskapet är också viktigt eftersom det är på dessa skalor som det bestäms hur mycket av den värdefulla veden som finns. Kontinuitet är viktigt åtminstone för vedskivlav och därför har även tidsskalan betydelse. Det är alltså tydligt att det är viktigt för skogsbruket att bli bättre på att säkra kontinuerlig tillgång på grov död ved samt för naturvården att bevara naturliga områden där sådan ved fortfarande finns kvar.

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Abbreviations

AIC	Akaike's information criteria
AIC_c	Akaike's information criteria corrected for sample size
C	*Cladonia parasitica*
DW	Deadwood
GLM	Generalised linear modelling
GLMM	Generalised linear mixed modelling
H	*Hertelidea botryosa*
WKH	Woodland key habitat

1. Introduction

Loss of habitat has large and consistently negative effects on biodiversity (Fahrig, 2003) and human-driven habitat destruction is the biggest cause of decline and extinction of species globally (Rockström et al., 2009). Species are heavily affected by habitat loss on the landscape level and not only on the local scale as the availability of habitat in the landscape determines the potential for recolonisation if the species should disappear from a local patch. e.g. through stochastic events such as disturbances (Fahrig, 2001).

The effects of habitat loss are however not always immediate. Especially for sessile species with a slow colonisation rate, such as lichens, there can be decades or even more than a century before the population reaches a new stable state after a habitat change; the delay constituting a so-called extinction debt (Kuussaari et al., 2009; Sverdrup-Thygeson et al., 2014). Kuussaari et al (2009) lists several ways to evaluate whether there is an extinction debt. One is to model occurrence of a species against past and present landscape characteristics. If the past landscape better explains species richness or occurrence of a species than the current one, we can assume that there is an extinction debt (Ellis & Coppins, 2007; Johansson et al., 2013). While this method does not tell us anything about the magnitude of the extinction debt, it is none the less advantageous in that it is relatively simple to procure the data necessary for the method. Evaluating the presence of extinction debt is important for nature conservation since not taking extinction debt into consideration might lead to faulty conclusions about the landscape's capacity to support species communities over time (Kuussaari et al., 2009).

Modern intensive forestry in Sweden has during the past century lead to loss of landscape diversity and to structural changes in the forest (Figure 1). Today, there is a lack of important structures for biodiversity, such as coarse deadwood and old trees, as well as old forest and continuity forest. This in turn has led to loss of species diversity or of lost genetic diversity within populations and in some cases, species have become lost (Esseen et al., 1997; Linder & Östlund, 1998). The situation is especially dire for species dependent on large deadwood dimensions in late decay stages since this is a substrate not recreated in modern forestry where almost all trees are extracted from the forest instead of being allowed to grow large and naturally die and decay in place (Gibb et al., 2005; Siitonen, 2001). Gibb et al. (2005)

showed that even though there is some DW on clearcuts and in managed forest, the large diameter classes and the late decay stages are largely missing even when the managed forest is old. This means that dead wood dependent species have lost much of their habitat in Sweden over the past century and though species tied to these substrates have still persisted in the landscape, an extinction debt may be present (Kuussaari et al., 2009; Sverdrup-Thygeson et al., 2014).

Figure 1. One of the surveyed woodland key habitats in Norrbotten. Hard, large diameter deadwood like this is rare in the intensively managed forest landscape of modern Sweden. Photo: Edith Bremer.

There are over 300 red-listed species in Scandinavia which depend on coarse and often naturally created deadwood for their survival, e.g. beetles, fungi and lichens, and lack of habitat and substrate in the form of continuity forest and deadwood of the right qualities is believed to be responsible for this development (Larsson et al., 2011). During the past decade, an increasing number of studies focusing on time-lagged effects of deadwood have appeared (Andersson et al., 2012; Berglund et al., 2011; Buse, 2012; Johansson et al., 2013; Nordén et al., 2013; Paltto et al., 2006). However, according to a review compiling these studies, lichens are underrepresented as these have mostly focused on beetles and, to some extent, fungi (Sverdrup-Thygeson et al., 2014). Previous studies on extinction debt in lichens include Berglund and Jonsson (2005), and Ellis and Coppins (2007). In the first example (Berglund & Jonsson, 2005) they found indications of extinction debt in microlichens on spruce in northern Sweden using reference stands. In the second example (Ellis & Coppins, 2007) they used historic landscape structure and found evidence of extinction debt in microlichens on aspen. This study will concern extinction debt in microlichens on pine and is, to my knowledge, the first study in Scandinavia to do so.

The aim of this study then, is to investigate the presence of an extinction debt on the deadwood-living microlichens *Cladonia parasitica* (Hoffm.) Hoffm. and *Hertelidea botryosa* (Fr.) Printzen & Kantvilas (hereafter called *C* and *H*) in northern Sweden. These species are both dependent on hard, large diameter pine deadwood (DW) in late decay stages and *H* also favours charred DW (Nitare, 2019). A previous study has shown that these species are more dependent on substrate quality than on stand characteristics (Källén, 2015). However, the landscape perspective has not been taken into consideration and this study therefore also aims to compare the importance of landscape scale effects with the substrate and stand scales by comparing the strengths of effects on each scale.

The questions I aim to answer are:

1) Is there an extinction debt for *Hertelidea botryosa* or *Cladonia parasitica?*
2) Is the occurrence of *Hertelidea botryosa* and *Cladonia parasitica* most strongly determined by landscape-, stand- or substrate characteristics*?*

2. Materials and methods

2.1. Study landscape and study species

During June and July 2020, I collected data from 55 old-growth forest stands in two different regions in northern Sweden: in central Norrbotten and at the borders between Västerbotten, Västernorrland and Jämtland (see map, Figure 1). Based on old data from the Swedish National Forest Inventories conducted in 1925 and 1955, these regions differ in their forest management history in that widespread clearcut-based forestry begun earlier in the southern than in the northern region (Swedish NFI, 1925, 1955). The surveyed stands were situated in pine dominated forests and mostly include woodland key habitats (WKH). In the southern region, WKHs were scarcer and there I surveyed a few nature reserves as well. The stands were a minimum of 1 ha in size, and at least 5km apart from each other. They were chosen so that the amount of old-growth forest (protected forests and key habitats) in the surrounding landscape varied. Stands close to roads were preferred in order to increase accessibility by car during fieldwork.

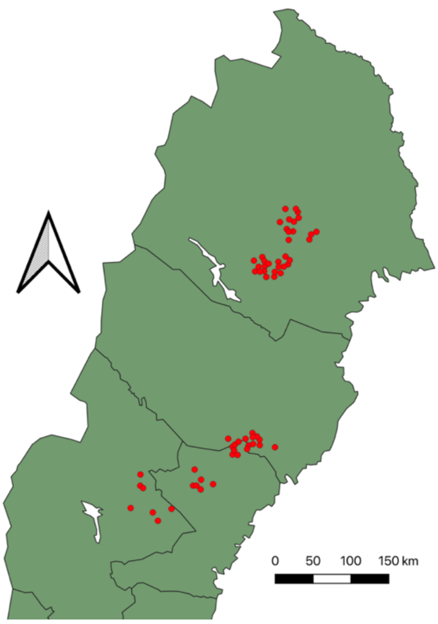


Figure 1. Map showing the surveyed areas in northern Sweden.

In all stands, I collected data on the amount of deadwood and on the occurrence of two lichen species, *Hertelidea botryosa* (*H*) and *Cladonia parasitica* (*C*) (Figure 2), that both have dead pine wood as their substrate, are red-listed in the near threatened-category and are easy to identify in the field. I walked transects of a total of 300 m within each stand, surveying every fallen log intersecting the line, and every standing dead tree within 10 m from the line. In order to calculate the average amount of dead wood in each stand, I measured the diameter of these trees and I assessed the decay stage on a scale from one to five using a knife and visual observation. I registered whether each surveyed DW was charred or not, as especially *H* is known to prefer this substrate (Nitare, 2019). I did the same for anthropogenic marks on the trees and also counted the number of cut stumps within 5 m of the transect to use as simple measures of forest management history within the stand. DW with a diameter <10 cm or a length <100cm were left out of the surveying process. To get an estimation of openness, I measured the basal area at four points in each stand.

Figure 2. Cladonia parasitica on the left (lower picture with apothecia) and Hertelidea botryosa on the right. Photos: Edith Bremer.

2.2. Landscape structure

Information on historic landscape structure was gathered from two sources: The first was the mapping of boreal Swedish continuity forests produced in 2016 by the Swedish EPA. This is a mapping of those forest stands that to date have not, or potentially have not, been clear-cut, and therefore are most likely to have forest continuity (Metria AB & Naturvårdsverket, 2017). The second was orthophotos of the landscape from 1960 available from Lantmäteriet (the Swedish mapping authority). Assuming all forest not recently clear cut or very young in 1960 was old forest, I could classify all these areas as possible habitat for the study species. A similar analysis of current landscape structure was obtained by using data from the Swedish Forest Agency on all areas clear cut between 2000 and 2019 and subtracting these from the total of forested areas. The continuity data describes long-term landscape structure whereas the snapshots of the landscape in 1960 and 2019 allows for comparison of importance by describing the landscape at discrete points in time. The different measures of habitat amount were calculated at several different landscape scales in order to find the scale most relevant for the species; within 300, 500, 1000 and 3000 m from the surveyed area in the stand. Previous studies have found landscape level effects at similar scales (Ellis & Coppins, 2009; Randlane et al., 2017; Svensson et al., 2013). Moreover, there was not time within the scope of this study to analyse larger scales. At smaller scales, the analysed landscapes would be the same as the surveyed stands which should all be old growth forests. All landscape structure analysis was made in QGIS3.10 (QGIS Development Team. 2018).

2.3. Data treatment and statistical analysis

2.3.1. Data treatment

The volume of standing and fallen deadwood was calculated separately. To calculate the amount of fallen deadwood, I used the line intersect sampling method (Marshal et al., 2000). For the standing deadwood, I used taper curve equations from Lassasenaho (1982) and scaled the numbers up to volume per hectare.

2.3.2. Generalised linear modelling

Using generalised linear modelling (GLM), I modelled the number of observations per stand in separate models for the two lichen species and examined the effect of landscape- and stand scale variables. I used a Poisson distribution for *C* and a negative binomial distribution for *H*. One observation was one piece of DW with either species occurring on them. All potential explanatory variables included in the model are presented in table 1. There was no collinearity between the different measures of habitat amount (variable inflation factor VIF <2.5). and they could all be included together. Including the region variable (stands' location in the north or south) increased the AIC of the model and this was therefore left out. For model simplicity, the number of cut stumps and the number of DW with anthropogenic marks was combined and included as total number of cut wood. The variables were standardized in order to enable comparisons of effect sizes (Gelman 2008). A set of models were then generated including all possible combinations of the explanatory variables and these were compared using Akaike's information criteria corrected for sample size (AICc). Model averaging was then performed with all models with a difference of AICc < 4 to estimate the effect sizes for each explanatory variable (Grueber et al. 2011). The component models included in the averaging are presented in appendix 1.

TABLE 1. Potential explanatory variables included in the GLMs and modelled against number of DW pieces with occurrence of H. botryosa and C. parasitica in the stands.

Landscape variables (proportions of the landscape at 300, 500, 1000 and 3000 m radius analysed in separate models)
Proportion of landscape forested 1960 Proportion of landscape forested 2019 Proportion of landscape continuity forest 2016
Stand-level variables
Volume/ha standing DW Volume/ha fallen DW Average basal area Average DW diameter Number of charred DW Number of cut DW (surveyed DW w. cutmarks + number of cut stumps)

2.3.3. Generalised linear mixed modelling

Results from the GLMs indicated that the properties of the substrate dead wood were the most important predictors of the lichens being present in a stand. In order to investigate these relationships more closely, I therefore went on to model the presence/absence of each species on a piece of DW using generalised linear mixed modelling (GLMM) with binomial distribution and logarithmic link function. This allowed me to examine the effect of characteristics of individual pieces of DW more closely. Since each surveyed piece of DW are not true replicates, stand was included as a random variable. The potential explanatory variables are shown in table 2. These are largely the same as in the GLM although the substrate variables are now included at the scale of individual deadwood items instead of stand scale. I excluded stump count and included cutmarks on surveyed DW as a separate variable since this gave a lower AIC here. Effects on the two species were again examined in separate models. Standardization of the variables and model selection by model averaging was performed in the same way as with the GLM analyses. The models included in the averaging are presented in appendix 3. Due to the uncertainties regarding interpretation of p-values in GLMM analyses, the 95% confidence interval is reported instead, and the effect of a variable is considered significant if the confidence interval differs from zero.

TABLE 2. Potential explanatory variables included in the GLMMs and modelled against the presence/absence of H. botryosa and C. parasitica on pieces of DW within the stands.

Landscape variables (proportions of the landscape at 300, 500, 1000 and 3000 m radius analysed in separate models)
Proportion of landscape forested 1960
Proportion of landscape forested 2019
Proportion of landscape continuity forest 2016
Stand-level variables
Volume/ha standing DW
Volume/ha fallen DW
Average basal area
Region (north/south)
Substrate-level variables
DW diameter
Charred DW (presence/absence)
Cut DW
Percent of DW covered by bark/bryophytes
Decay stage (1-5)
Deadwood type (standing/fallen)

All statistical analyses were performed with R 4.0.3 (RCore Team, 2020), using packages lme4 (Bates et al., 2015), MuMIn (Barton, 2016), arm (Gelman et al., 2020), and car (Fox & Weisberg, 2011).

3. Results

1157 pieces of DW in 55 stands were surveyed (33 stands in the northern and 22 in the southern region). Out of these, 395 were fallen and 762 were standing DW. *H* and *C* occurred on 99 and 142 DW pieces respectively.

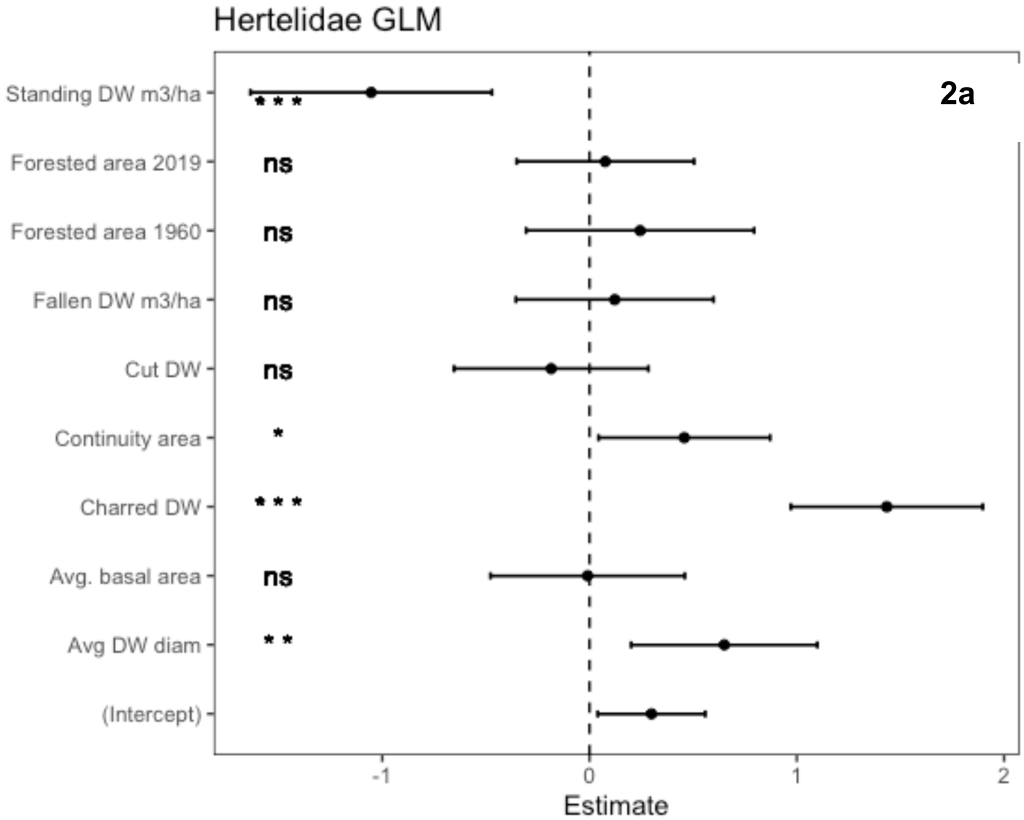
3.1. GLM

3.1.1. Landscape scale

None of the landscape variables had any strong correlation with either species. However, a weak positive effect on *H* was observed with increasing proportions of continuity forest. This effect was significant on the two smallest landscape levels (300m: est. 0.46, SE 0.21, p. 0.03 (Figure 2a, Appendix 2); 500m: est. 0.42, SE 0.20, p. 0.04 (Appendix 2)). Similarly, there was a weak positive effect on *C* with increasing forested proportion of the landscape in 2019. This too was only significant on the smaller landscape levels (300m: est. 0.43, SE 0.19, p. 0.03 (Figure 2b. Appendix 2); 500m: est. 0.42, SE 0.20, p. 0.04 (Appendix 2)). Since the strongest effects were observed on the 300m level, results on the stand level will be reported below from the model using the 300m radius landscape variables. The results from the other landscape levels can be found in appendix 2.

3.1.2. Stand scale

On the stand level, *H* was positively correlated with the amount of charred wood (est. 1.43, SE 0.23, p. <0.001) and with the average DW diameter (est. 0.65, SE 0.22, p. 0.005). It was negatively correlated with the volume of standing pine DW (est. -1.05, SE 0.29, p. <0.001). *C* was positively correlated with the amount of charred wood (est. 1.55, SE 0.20, p. <0.001) and with the volume of fallen pine DW (est. 0.73, SE 0.19, p. <0.001). It too was negatively correlated with the volume of standing pine DW (est. -1.12, SE 0.31, p. <0.001). The average basal area and the amount of cut wood had no effect on either species.



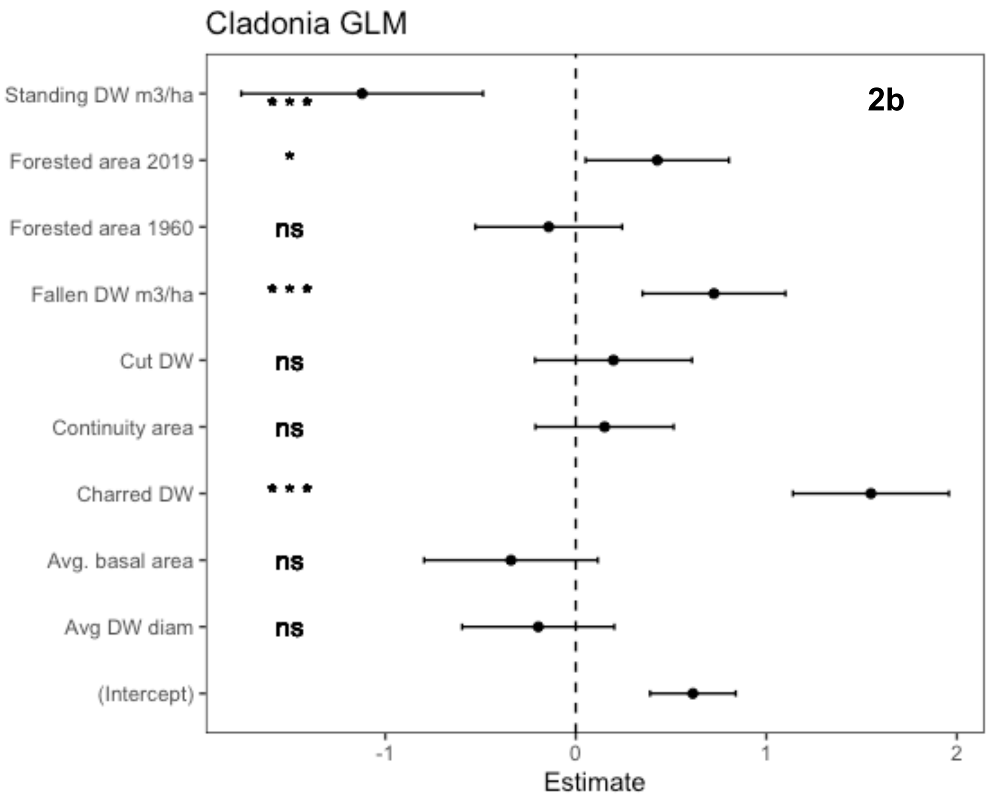


*Figure 1: From the conditional average for the GLM of Hertelidea occurrence (2a) and Cladonia occurrence (2b); The model-averaged parameter estimates with 95% confidence interval and with the significance level indicated as *** = < 0.001. ** = 0.005. * = 0.05 and ns = not significant.*

3.2. GLMM

3.2.1. Landscape scale

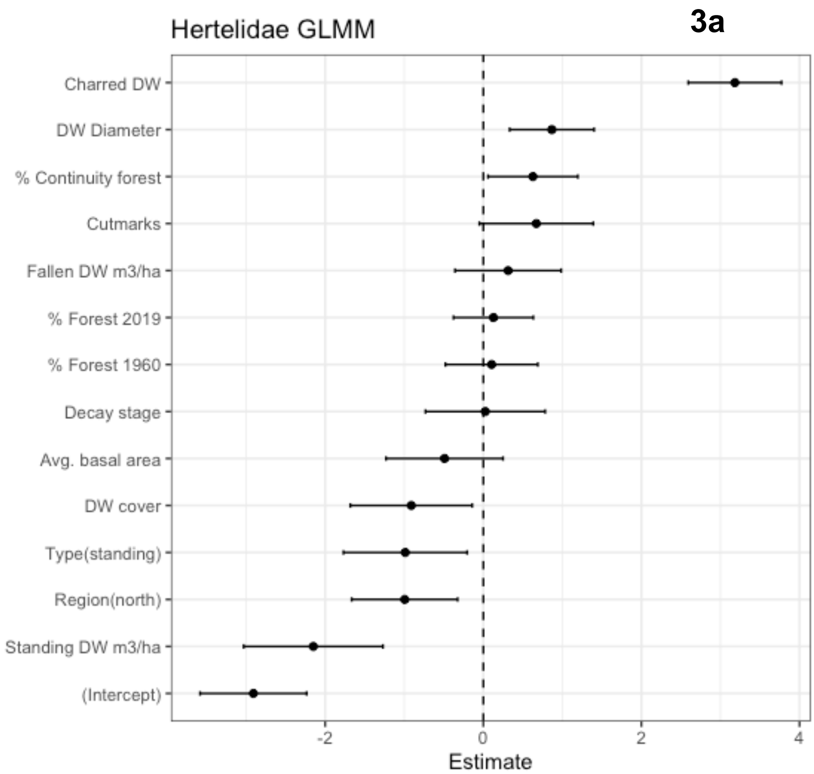
There was a stronger positive effect of the amount of continuity forest within 300 m on the chance of *H* occurring on a single piece of DW (est. 0.62) (Figure 3a, Appendix 4) than on the number of *H* occurring within a stand (Figure 2a). The amount of old forest habitat in 1960 and 2019 again had no effect. *C* in this analysis was not significantly affected by any of the landscape level variables. Though there was a positive trend with the amount of continuity forest within 300m (est. 0.59) (Figure 3b, Appendix 4) this was not significant since the 95 % confidence interval did not differ from zero.

3.2.2. Stand scale

The chance of *H* occurring on any one piece of DW decreased with the volume of standing pine DW (est. -2.15). The same was true if the stand was situated in the northern study region (est. -0.99). For *C* the only significant stand-level effect was the negative correlation with standing pine DW (est. -1.82). The average basal area and volume of fallen pine DW had no significant effect on either species.

3.2.3. Substrate scale

The most important factor determining whether *H* occurred or not was whether the DW was charred (est. 3.18). *H* also occurred more often when the DW was fallen (standing est. -0.99), had a larger diameter (est. 0.87) and was less covered with bark or bryophytes (cover est. -0.91). The occurrence of *C* was affected by all substrate-level variables in the model. It was most important that the DW be fallen (standing est. -3.25), followed by less cover (cover est. -2.14). It was also more likely to occur when the DW was charred (est. 1.63), had anthropogenic marks (est. 0.77), a larger diameter (est. 0.93) and a higher decay stage (est. 1.24).



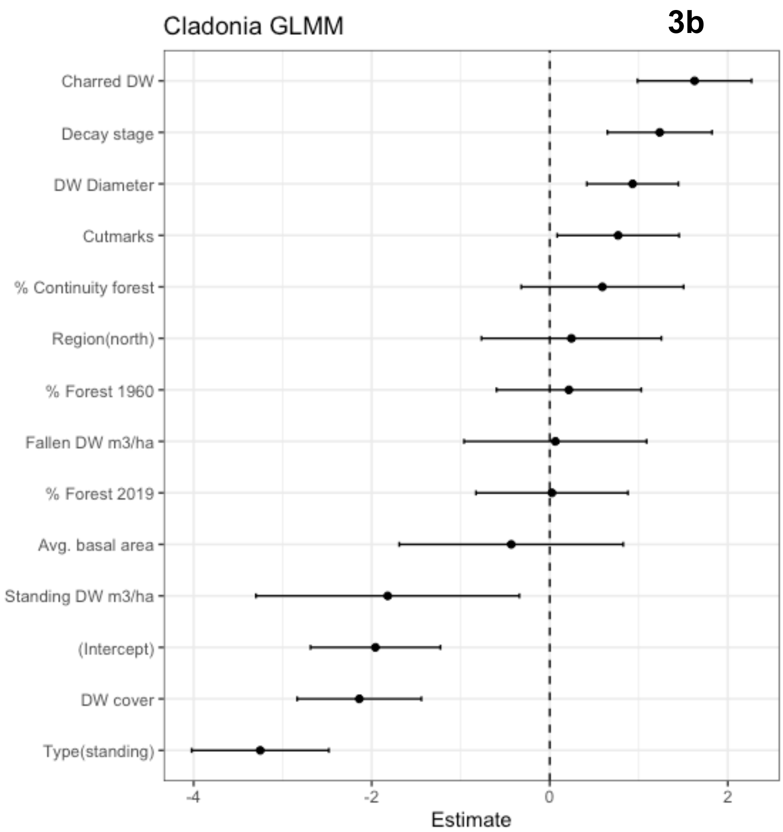


Figure 2: From the conditional average for the GLMM of Hertelidea occurrence (2a) and Cladonia occurrence (2b); The model-averaged parameter estimates with 95% confidence interval.

4. Discussion

4.1. Extinction debt

No extinction debt could be detected for *Hertelidea botryosa* by comparing available habitat in the form of old forest in 1960 and 2019 as *H* had no correlation with habitat amount in either time period. Association of a species with amount of continuity forest in the landscape can sometimes be interpreted as evidence of extinction debt (B. Nordén et al., 2014). Though I cannot rule this out as part of the explanation, it is more likely in this case that the continuity data simply describes the habitat requirements for *H* better than the snapshots of available forest habitat in 1960 and 2019. The forest classified as habitat in the snapshots includes many different types of forest, from protected to managed. The continuity forest data on the other hand, should only include old forest which is much more likely to include the type of DW that *H* needs (Gibb et al., 2005). Thus, we can only conclude that the occurrence of *H*, both their number in a stand (GLM analysis) and the chance of them occurring on individual pieces of DW (GLMM analysis), is positively associated with the *current* amount of available habitat in the form of continuity forest. As for *Cladonia parasitica*, the number of DW with *C* in a stand (GLM analysis) was correlated with current habitat amount measured as all mature forest in 2019, an effect that was not visible on the scale of individual pieces of DW within the stands (GLMM analysis), where there was instead a non-significant positive trend with continuity. This again indicates that the continuity data in this case does not point towards extinction debt but instead describes current habitat availability, and in the case of *H* does so better than data on amount of forested area in general. As no data on amount of continuity forest in the past was available in this case, no comparison to detect extinction debt using this measurement of habitat could be made and thus, this study can neither confirm no refute extinction debt in either species. However, the temporal scale is still important as continuity, by definition, has everything to do with time.

These landscape structure effects were only detectable on the smallest scales (300-500 m). It is possible that the real scale of effect is even smaller (Jackson & Fahrig, 2015). On the minute scale of a microlichen, long-term survival might not be so much about colonizing new forest stands in a managed landscape, but more about colonizing new deadwood in stands full of living trees and the variables used here to describe past, present and continuous habitat availability might therefore not fit the studied species. To find the scale of effect, one might consider using the continuity data on a smaller scale than the 300 m radius. However, while working in GIS, I was able to observe that the continuity data set was not always correct. There were cases where areas that were clearly deforested in 1960 were marked as continuity forest. This data then, is perhaps not accurate enough to be used on the 300 – 500m or smaller radius that is relevant for these species. A recent study (Lundmark et al., 2021) also showed that clear-cutting was already widespread in some parts of northern Sweden decades before 1960s and that using aerial photos starting from the this time (as done in this study and in the forest continuity data from the Swedish EPA) can lead to false classification of second-generation forest as continuity forest. With this type of data then, it might not be possible classify habitat on small enough scales, nor the type of habitat (in the form of forest with continuity of course DW availability) that is relevant for this type of species. In this case, comparing past and present habitat amount might not therefore be the best method of evaluating extinction debt. Indeed, the only previous boreal study that researched and was able to confirm extinction debt in lichens used reference stands rather comparing conditions past and present (Berglund & Jonsson, 2005). Sverdrup-Thygeson et al. (2014) strongly recommends future studies on extinction debt in dead wood dependent species to extend research to areas of forest with natural levels of course DW, such as parts of Russia, Canada and Alaska, and to use these as reference landscapes.

4.2. Which scale is most important?

Though the stand-level variables such as the volume of DW had some effect, it was substrate level variables such as the type of DW (fallen), the proportion covered by bark/bryophytes, whether the deadwood was charred, decay stage and diameter that were most important. This was true for both species and might therefore be true for DW dependent microlichens as a group. This corroborates previous knowledge on the substrate requirements of these species (Källén, 2015; Nitare, 2019). Källén (2017) also reported the same relationship between substrate- and stand scale effects for the same species. The only effect that stood out compared to previous knowledge was that *C* was more likely to occur on DW with anthropogenic marks. This can probably be attributed to the cut DW being older than average, i.e. having a larger diameter (overall avg. DW diam.: 19.3 ±0.2 cm; cut DW avg. diam. 27.4 ±0.7 cm). While in the field, I was able to observe that most of these anthropogenic marks were the remnants of old bark peelings, or else trees cut down to provide hanging lichens for reindeer. These kinds of traces of older human influence in the forest is common in northern Sweden and are mostly found on old, large diameter trees (Bergman, 2011; Zackrisson et al., 2000).

The landscape level effects were relatively small but as discussed above, this might be ascribable to the methods of classifying habitat not fitting the species well enough. Studies comparing the importance of different spatial scales for deadwood dependent beetles have shown varied and often species specific results where either the landscape-, stand- or substrate scale has stood out as most important or else species have responded to combinations of some or all of these scales (Jackson et al., 2012; Kehler et al., 1999; Økland et al., 1996; Rukke & Midtgaard, 1998; Saint-Germain & Drapeau, 2011). Similar studies on lichens are rare and I have found no previous research focused on comparing landscape-, stand- and substrate scale effects on dead wood dependent lichens. However, similar results as in this study has been presented for epiphytic lichens in general where Hungarian studies has found that effects on multiple scales interact to shape lichen species richness, with the substrate scale being of greatest importance followed by stand-scale and with effects on the landscape level being almost nonexistent (Király et al., 2013; Nascimbene et al., 2012). Just as I did in my snapshots of past and present habitat amount, these studies only measured the amount of forest cover in the landscape, not taking the quality of this habitat into consideration.

The most important stand-level variable was the amount of standing DW m^3/ha which had a strong negative effect. This is probably a sampling effect since both species were more likely to occur on fallen than on standing DW and I surveyed about twice as much standing as fallen DW. Considering that both species preferred fallen DW, one might have assumed that the volume of fallen DW/ha should have had a positive influence on species occurrence (Lassauce et al., 2011; Radu, 2007). Such an effect was only visible in the GLM for *C*. The absence of such an effect in the other analyses could be due to the variation in DW amount between stands being too small to detect any such effects. WKHs in Sweden have lower DW volumes than old growth forests (Jönsson & Jonsson, 2007). This was true in this study too where the surveyed sites had 14.47 ± 1.31 m^3. In old growths forests in this study's southern surveyed region, typical fallen DW volumes are around 25 m^3/ha (Gibb et al., 2005). As very few of the stands had DW volumes at a level typically found in old growth forests, and as these forests are seen as the typical habitat for these species (Nitare, 2019), it is likely that the volume of fallen DW is limiting, as the *C* GLM suggests, and the stand scale therefore cannot be forgotten in forestry and conservation planning (Bauhus et al., 2009; Santaniello, Djupström, Ranius, Weslien, Rudolphi, & Sonesson, 2017).

4.3. Conclusions

As is true for many species groups (Grove, 2002; Junninen & Komonen, 2011; Santaniello, Djupström, Ranius, Weslien, Rudolphi, & Thor, 2017), the results from this study supports previous knowledge that substrate level characteristics such as DW diameter, decay stage and the presence of charred wood is most important for DW-dependent microlichens (Källén, 2015; Nitare, 2019). The detected landscape level effects showed positive association with current habitat amounts in the form of continuity forest for *Hertelidea botryosa* and forest older than 20 years for *Cladonia parasitica*. Extinction debt could neither be confirmed nor refuted based on these results. The landscape scale effects were small compared to the substrate scale but were more important than some stand scale variables. Future studies could yield clearer results on landscape level effects by defining habitat more by availability or continuity of specific types of DW (fallen, large diameter, charred, late decay stage, little cover) than by age or continuity of the forest. Due to the difficulties of defining such habitat on a historic scale, extinction debt in species with these types of habitat/substrate requirements might be better to research using reference landscapes in areas with natural DW levels (Berglund & Jonsson, 2005; Sverdrup-Thygeson et al., 2014).

All scales matter, spatial as well as temporal. Even though the total amount of DW in managed forest has increased over the past decades as forestry has gone through some reformation, the type of deadwood needed for these and many other species is very difficult to create in managed forests; even if prescribed fire or similar methods are used (Santaniello, Djupström, Ranius, Weslien, Rudolphi, & Thor, 2017). This study again underlines the need for forestry to increase their efforts to make sure that high quality DW is continually recreated (Jonsson et al., 2005) and for conservation efforts to preserve the few areas where this DW is still naturally recreated.

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Appendix 1

Component models included in the Hertelidea GLM model averaging (deltaAICc < 4). Parameters explained in table 1.

300 m	df	logLik	AICc	delta	weight
Avg DW diam. + Charred + Continuity + Standing DW	6	-77.29	168.33	0.00	0.33
Avg DW diam. + Charred + Continuity + 1960 forest + Standing DW	7	-76.94	170.27	1.94	0.12
Avg DW diam. + Charred + Cut wood + Continuity + Standing DW	7	-76.97	170.33	2.00	0.12
Avg DW diam. + Charred + Fallen DW + Continuity + Standing DW	7	-77.16	170.70	2.37	0.10
Avg DW diam. + Charred + Standing DW	5	-79.79	170.81	2.48	0.09
Avg DW diam. + Charred + Continuity + 2019 forest + Standing DW	7	-77.22	170.83	2.50	0.09
Avg basal area + Avg DW diam. + Charred + Continuity + Standing DW	7	-77.29	170.96	2.63	0.09
Avg DW diam. + Charred + 1960 forest + Standing DW	6	-79.15	172.05	3.72	0.05
500 m	df	logLik	AICc	delta	weight
Avg DW diam. + Charred + Continuity + Standing DW	6	-77.48	168.71	0.00	0.32
Avg DW diam. + Charred + Cut wood + Continuity + Standing DW	7	-77.14	170.66	1.95	0.12
Avg DW diam. + Charred + Continuity + 1960 forest + Standing DW	7	-77.14	170.66	1.96	0.12
Avg DW diam. + Charred + Standing DW	5	-79.79	170.81	2.10	0.11
Avg DW diam. + Charred + Fallen DW + Continuity + Standing DW	7	-77.33	171.04	2.34	0.10
Avg DW diam. + Charred + Continuity + 2019 forest + Standing DW	7	-77.46	171.29	2.59	0.09
Avg basal area + Avg DW diam. + Charred + Continuity + Standing DW	7	-77.48	171.34	2.63	0.08
Avg DW diam. + Charred + 1960 forest + Standing DW	6	-79.06	171.86	3.16	0.07
1 km	df	logLik	AICc	delta	weight
Avg DW diam. + Charred + Continuity + Standing DW	6	-78.09	169.92	0.00	0.17
Avg DW diam. + Charred + Standing DW	5	-79.79	170.81	0.88	0.11

Avg DW diam. + Charred + Continuity + 1960 forest + Standing DW	7	-77.36	171.11	1.19	0.09
Avg DW diam. + Charred + 1960 forest + Standing DW	6	-78.82	171.39	1.46	0.08
Avg DW diam. + Charred + Cut wood + Continuity + Standing DW	7	-77.62	171.63	1.70	0.07
Avg DW diam. + Charred + Fallen DW + Continuity + Standing DW	7	-77.89	172.17	2.25	0.05
Avg DW diam. + Charred + Continuity + 2019 forest + Standing DW	7	-78.01	172.39	2.47	0.05
Avg basal area + Avg DW diam. + Charred + Continuity + Standing DW	7	-78.08	172.54	2.61	0.05
Avg DW diam. + Charred + Fallen DW + Standing DW	6	-79.50	172.74	2.82	0.04
Avg DW diam. + Charred + Cut wood + Standing DW	6	-79.56	172.87	2.95	0.04
Avg basal area + Avg DW diam. + Charred + Standing DW	6	-79.63	173.01	3.08	0.04
Avg DW diam. + Charred + 2019 forest + Standing DW	6	-79.63	173.01	3.09	0.04
Avg DW diam. + Charred + Cut wood + Continuity + 1960 forest + Standing DW	8	-77.16	173.46	3.53	0.03
Avg DW diam. + Charred + Fallen DW + Continuity + 1960 forest + Standing DW	8	-77.19	173.52	3.60	0.03
Avg DW diam. + Charred + Fallen DW + 1960 forest + Standing DW	7	-78.57	173.52	3.60	0.03
Avg basal area + Avg DW diam. + Charred + 1960 forest + Standing DW	7	-78.58	173.55	3.63	0.03
Avg basal area + Avg DW diam. + Charred + Continuity + 1960 forest + Standing DW	8	-77.33	173.79	3.87	0.02
Avg DW diam. + Charred + Continuity + 1960 forest + 2019 forest + Standing DW	8	-77.36	173.85	3.93	0.02
Avg DW diam. + Charred + Cut wood + 1960 forest + Standing DW	7	-78.76	173.90	3.98	0.02

3 km	df	logLik	AICc	delta	weight
Avg DW diameter + Charred + Standing DW	5	-79.79	170.81	0.00	0.18
Avg DW diameter + Charred + 1960 forest + Standing DW	6	-78.65	171.06	0.25	0.16
Avg DW diameter + Charred + Continuity + Standing DW	6	-79.30	172.35	1.54	0.08
Avg DW diameter + Charred + Fallen DW + Standing DW	6	-79.50	172.74	1.93	0.07
Avg DW diameter + Charred + Cut wood + Standing DW	6	-79.56	172.87	2.06	0.06
Avg basal area + Avg DW diameter + Charred + Standing DW	6	-79.63	173.01	2.20	0.06
Avg DW diameter + Charred + Continuity + 1960 forest + Standing DW	7	-78.44	173.27	2.47	0.05
Avg DW diameter + Charred + 2019 forest + Standing DW	6	-79.77	173.28	2.48	0.05
Avg DW diameter + Charred + Fallen DW + 1960 forest + Standing DW	7	-78.46	173.29	2.49	0.05
Avg DW diameter + Charred + Cut wood + 1960 forest + Standing DW	7	-78.57	173.53	2.72	0.05
Avg basal area + Avg DW diameter + Charred + 1960 forest + Standing DW	7	-78.58	173.55	2.75	0.05
Avg DW diameter + Charred + 1960 forest + 2019 forest + Standing DW	7	-78.59	173.55	2.75	0.05
Charred + 1960 forest + Standing DW	5	-81.23	173.68	2.87	0.04
Avg DW diameter + Charred + Cut wood + Continuity + Standing DW	7	-78.86	174.11	3.30	0.03
Avg DW diameter + Charred + Fallen DW + Continuity + Standing DW	7	-79.13	174.65	3.85	0.03

Component models included in the Cladonia GLM model averaging (deltaAICc < 4). Parameters explained in table 1.

300 m	df	logLik	AICc	delta	weight
Charred + Fallen DW + nitton forest + Standing DW	5	-102.50	216.22	0.00	0.15
Avg basal area + Charred + Fallen DW + nitton forest + Standing DW	6	-101.36	216.47	0.25	0.13
Avg DW diam. + Charred + Fallen DW + nitton forest + Standing DW	6	-101.89	217.52	1.31	0.08
Avg basal area + Charred + Cut wood + Fallen DW + nitton forest + Standing DW	7	-100.72	217.82	1.60	0.07
Charred + Fallen DW + Continuity + nitton forest + Standing DW	6	-102.08	217.90	1.68	0.07
Charred + Cut wood + Fallen DW + nitton forest + Standing DW	6	-102.24	218.23	2.01	0.06
Charred + Fallen DW + sexti forest + nitton forest + Standing DW	6	-102.29	218.33	2.12	0.05
Avg basal area + Charred + Fallen DW + sexti forest + nitton forest + Standing DW	7	-101.01	218.41	2.19	0.05
Avg basal area + Avg DW diam. + Charred + Fallen DW + nitton forest + Standing DW	7	-101.12	218.63	2.41	0.05
Avg basal area + Charred + Fallen DW + Continuity + nitton forest + Standing DW	7	-101.18	218.74	2.52	0.04
Avg basal area + Charred + Fallen DW + Standing DW	5	-103.88	218.98	2.77	0.04
Avg DW diam. + Charred + Fallen DW + Continuity + nitton forest + Standing DW	7	-101.50	219.39	3.17	0.03
Avg DW diam. + Charred + Cut wood + Fallen DW + nitton forest + Standing DW	7	-101.51	219.39	3.18	0.03
Charred + Fallen DW + Standing DW	4	-105.38	219.56	3.34	0.03
Avg basal area + Charred + Cut wood + Fallen DW + Standing DW	6	-102.92	219.59	3.37	0.03
Avg DW diam. + Charred + Fallen DW + sexti forest + nitton forest + Standing DW	7	-101.62	219.62	3.40	0.03
Avg basal area + Avg DW diam. + Charred + Cut wood + Fallen DW + nitton forest + Standing DW	8	-100.41	219.94	3.72	0.02
Charred + Fallen DW + Continuity + sexti forest + nitton forest + Standing DW	7	-101.81	220.00	3.79	0.02
Charred + Cut wood + Fallen DW + Continuity + nitton forest + Standing DW	7	-101.86	220.10	3.88	0.02
500 m	**df**	**logLik**	**AICc**	**delta**	**weight**
Charred + Fallen DW + 2019 forest + Standing DW	5	-102.85	216.92	0.00	0.15
Avg basal area + Charred + Fallen DW + 2019 forest + Standing DW	6	-101.99	217.73	0.81	0.10
Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	6	-102.18	218.12	1.20	0.08
Avg basal area + Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	7	-101.10	218.58	1.66	0.07
Avg DW diam. + Charred + Fallen DW + 2019 forest + Standing DW	6	-102.43	218.60	1.68	0.06
Charred + Cut wood + Fallen DW + 2019 forest + Standing DW	6	-102.46	218.67	1.75	0.06
Avg basal area + Charred + Cut wood + Fallen DW + 2019 forest + Standing DW	7	-101.22	218.82	1.90	0.06
Avg basal area + Charred + Fallen DW + Standing DW	5	-103.88	218.98	2.06	0.05
Charred + Fallen DW + Continuity + 2019 forest + Standing DW	6	-102.85	219.44	2.52	0.04
Charred + Fallen DW + Standing DW	4	-105.38	219.56	2.64	0.04
Avg basal area + Charred + Cut wood + Fallen DW + Standing DW	6	-102.92	219.59	2.66	0.04

Avg DW diam. + Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	7	-101.70	219.79	2.87	0.04
Avg basal area + Avg DW diam. + Charred + Fallen DW + 2019 forest + Standing DW	7	-101.82	220.02	3.10	0.03
Avg DW diam. + Charred + Cut wood + Fallen DW + 2019 forest + Standing DW	7	-101.92	220.23	3.30	0.03
Avg basal area + Charred + Fallen DW + Continuity + 2019 forest + Standing DW	7	-101.94	220.26	3.33	0.03
Avg basal area + Charred + Fallen DW + 1960 forest + Standing DW	6	-103.26	220.27	3.35	0.03
Charred + Cut wood + Fallen DW + 1960 forest + 2019 forest + Standing DW	7	-102.09	220.57	3.64	0.02
Avg basal area + Charred + Cut wood + Fallen DW + 1960 forest + 2019 forest + Standing DW	8	-100.77	220.67	3.74	0.02
Avg DW diam. + Charred + Fallen DW + Standing DW	5	-104.74	220.71	3.79	0.02
Charred + Fallen DW + Continuity + 1960 forest + 2019 forest + Standing DW	7	-102.18	220.75	3.82	0.02
1 km	df	logLik	AICc	delta	weight
Avg basal area + Charred + Fallen DW + 1960 forest + Standing DW	6	-102.05	217.86	0.00	0.13
Charred + Fallen DW + 1960 forest + Standing DW	5	-103.64	218.50	0.64	0.10
Avg basal area + Charred + Fallen DW + Standing DW	5	-103.88	218.98	1.13	0.08
Charred + Fallen DW + Standing DW	4	-105.38	219.56	1.70	0.06
Avg basal area + Charred + Cut wood + Fallen DW + Standing DW	6	-102.92	219.59	1.73	0.06
Avg basal area + Charred + Cut wood + Fallen DW + 1960 forest + Standing DW	7	-101.73	219.83	1.98	0.05
Avg DW diam. + Charred + Fallen DW + 1960 forest + Standing DW	6	-103.07	219.89	2.03	0.05
Avg basal area + Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	7	-101.81	220.00	2.14	0.05
Avg basal area + Charred + Fallen DW + Continuity + 1960 forest + Standing DW	7	-101.82	220.03	2.17	0.05
Avg basal area + Avg DW diam. + Charred + Fallen DW + 1960 forest + Standing DW	7	-101.88	220.14	2.28	0.04
Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	6	-103.25	220.24	2.39	0.04
Avg DW diam. + Charred + Fallen DW + Standing DW	5	-104.74	220.71	2.86	0.03
Avg basal area + Charred + Fallen DW + Continuity + Standing DW	6	-103.51	220.77	2.92	0.03
Avg basal area + Charred + Cut wood + Fallen DW + Continuity + Standing DW	7	-102.21	220.81	2.95	0.03
Charred + Fallen DW + Continuity + 1960 forest + Standing DW	6	-103.56	220.87	3.02	0.03
Charred + Cut wood + Fallen DW + 1960 forest + Standing DW	6	-103.63	221.00	3.15	0.03
Avg basal area + Avg DW diam. + Charred + Fallen DW + Standing DW	6	-103.64	221.04	3.18	0.03
Charred + Cut wood + Fallen DW + Standing DW	5	-105.05	221.32	3.46	0.02
Avg basal area + Charred + Fallen DW + 2019 forest + Standing DW	6	-103.83	221.40	3.54	0.02
Avg basal area + Avg DW diam. + Charred + Cut wood + Fallen DW + Standing DW	7	-102.59	221.56	3.70	0.02
Avg basal area + Charred + Cut wood + Fallen DW + Continuity + 1960 forest + Standing DW	8	-101.27	221.68	3.82	0.02
Charred + Fallen DW + Continuity + Standing DW	5	-105.24	221.71	3.85	0.02
Charred + Fallen DW + 2019 forest + Standing DW	5	-105.27	221.77	3.91	0.02

3 km	df	logLik	AICc	delta	weight
Avg basal area + Charred + Fallen DW + Standing DW	5	-103.88	218.98	0.00	0.14
Charred + Fallen DW + Standing DW	4	-105.38	219.56	0.58	0.11
Avg basal area + Charred + Cut wood + Fallen DW + Standing DW	6	-102.92	219.59	0.60	0.11
Avg basal area + Charred + Fallen DW + 1960 forest + Standing DW	6	-103.46	220.67	1.69	0.06
Avg DW diam. + Charred + Fallen DW + Standing DW	5	-104.74	220.71	1.73	0.06
Avg basal area + Charred + Fallen DW + 2019 forest + Standing DW	6	-103.49	220.72	1.74	0.06
Avg basal area + Avg DW diam. + Charred + Fallen DW + Standing DW	6	-103.64	221.04	2.05	0.05
Avg basal area + Charred + Cut wood + Fallen DW + 2019 forest + Standing DW	7	-102.33	221.05	2.07	0.05
Avg basal area + Charred + Fallen DW + Continuity + Standing DW	6	-103.77	221.30	2.31	0.04
Charred + Cut wood + Fallen DW + Standing DW	5	-105.05	221.32	2.34	0.04
Avg basal area + Charred + Cut wood + Fallen DW + Continuity + Standing DW	7	-102.47	221.33	2.35	0.04
Avg basal area + Avg DW diam. + Charred + Cut wood + Fallen DW + Standing DW	7	-102.59	221.56	2.58	0.04
Charred + Fallen DW + 1960 forest + Standing DW	5	-105.22	221.66	2.68	0.04
Charred + Fallen DW + 2019 forest + Standing DW	5	-105.22	221.67	2.68	0.04
Avg basal area + Charred + Cut wood + Fallen DW + 1960 forest + Standing DW	7	-102.73	221.84	2.86	0.03
Charred + Fallen DW + Continuity + Standing DW	5	-105.38	221.98	3.00	0.03
Avg DW diam. + Charred + Cut wood + Fallen DW + Standing DW	6	-104.25	222.25	3.27	0.03
Avg basal area + Charred + Fallen DW + 1960 forest + 2019 forest + Standing DW	7	-103.28	222.94	3.95	0.02

Appendix 2

The model-averaged parameter estimates with standard error and p-values from the conditional average for the GLM of Hertelidea occurrence. Presented in order of strength of effect (estimate farthest from zero) in the 300 m model. Parameters explained in table 1.

HERTELIDAE	300 m			500 m			1 km			3 km		
	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)
(Intercept)	0.30	0.13	0.02	0.31	0.13	0.02	0.32	0.13	0.01	0.33	0.12	0.01
Charred	1.43	0.23	<0.001	1.38	0.23	<0.001	1.40	0.22	<0.001	1.38	0.23	<0.001
Standing DW	-1.05	0.29	<0.001	-0.99	0.28	<0.001	-0.98	0.28	<0.001	-0.91	0.29	<0.001
Avg diam.	0.65	0.22	0.005	0.64	0.22	0.01	0.59	0.22	0.01	0.56	0.23	0.02
Continuity forest	0.46	0.21	0.03	0.42	0.20	0.04	0.37	0.20	ns	0.20	0.22	ns
1960 forest	0.24	0.27	ns	0.25	0.27	ns	0.31	0.25	ns	0.35	0.24	ns
Cut wood	-0.18	0.23	ns	-0.19	0.23	ns	-0.18	0.24	ns	-0.15	0.24	ns
Fallen DW	0.12	0.24	ns	0.13	0.24	ns	0.16	0.23	ns	0.16	0.23	ns
2019 forest	0.08	0.21	ns	0.05	0.22	ns	0.09	0.23	ns	-0.02	0.25	ns
Avg basal area	-0.01	0.23	ns	-0.01	0.23	ns	-0.09	0.24	ns	-0.11	0.23	ns

The model-averaged parameter estimates with standard error and p-values from the conditional average for the GLM of Cladonia occurrence. Presented in order of strength of effect (estimate farthest from zero) in the 300 m model. Parameters explained in table 1.

CLADONIA	300 m			500 m			1 km			3 km		
	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)	Estimate	SE	Pr(>|z|)
(Intercept)	0.61	0.11	0.00	0.62	0.11	0.00	0.63	0.11	<0.001	0.63	0.11	<0.001
Charred	1.55	0.20	<0.001	1.56	0.21	<0.001	1.53	0.20	<0.001	1.50	0.20	<0.001
Standing DW	-1.12	0.32	<0.001	-1.14	0.32	<0.001	-1.01	0.33	0.003	-1.01	0.34	0.003
Fallen DW	0.73	0.19	<0.001	0.73	0.19	<0.001	0.76	0.19	<0.001	0.78	0.19	<0.001
2019 forest	0.43	0.19	0.03	0.42	0.20	0.04	0.13	0.20	ns	-0.17	0.21	ns
Avg basal area	-0.34	0.23	ns	-0.34	0.23	ns	-0.40	0.23	ns	-0.43	0.24	ns
Avg diam.	-0.20	0.20	ns	-0.18	0.20	ns	-0.17	0.21	ns	-0.19	0.21	ns
Cut wood	0.20	0.21	ns	0.21	0.21	ns	0.22	0.23	ns	0.27	0.21	ns
Continuity forest	0.15	0.18	ns	-0.02	0.17	ns	-0.13	0.17	ns	-0.10	0.20	ns
1960 forest	-0.14	0.19	ns	-0.22	0.19	ns	-0.32	0.17	ns	-0.13	0.17	ns

Appendix 3

Component models included in the Hertelidea GLMM model averaging (deltaAICc < 4). Stand is included as random variable in all models. Parameters explained in table 2.

Model	df	logLik	AICc	delta AICc	weight
Charred + Continuity + Cover + Cuts + Diam. + Region + Standing/ha + Type	10	-209.236	438.7	0.00	0.093
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Region + Standing/ha + Type	11	-208.317	438.9	0.20	0.084
Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Region + Standing/ha + Type	11	-208.702	439.6	0.97	0.057
Charred + Continuity + Cover + Diam. + Region + Standing/ha + Type	9	-210.796	439.7	1.09	0.054
Avg basal area + Charred + Continuity + Cover + Diam. + Region + Standing/ha + Type	10	-209.952	440.1	1.43	0.045
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Region + Standing/ha + Type	12	-207.960	440.2	1.53	0.043
Charred + Continuity + Cover + Cuts + Diam. + Forest 2019 + Region + Standing/ha + Type	11	-209.120	440.5	1.81	0.038
Charred + Continuity + Cover + Cuts + Diam. + Forest 1960 + Region + Standing/ha + Type	11	-209.152	440.5	1.87	0.037
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Forest 2019 + Region + Standing/ha + Type	12	-208.202	440.7	2.01	0.034
Charred + Continuity + Cover + Cuts + Decay + Diam. + Region + Standing/ha + Type	11	-209.235	440.7	2.04	0.034
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Forest 1960 + Region + Standing/ha + Type	12	-208.259	440.8	2.13	0.032
Avg basal area + Charred + Continuity + Cover + Cuts + Decay + Diam. + Region + Standing/ha + Type	12	-208.317	440.9	2.24	0.030
Charred + Continuity + Cover + Diam. + Fallen/ha + Region + Standing/ha + Type	10	-210.366	440.9	2.26	0.030
Charred + Cover + Cuts + Diam. + Region + Standing/ha + Type	9	-211.490	441.1	2.47	0.027
Charred + Continuity + Cover + Diam. + Forest 2019 + Region + Standing/ha + Type	10	-210.570	441.3	2.67	0.025

Avg basal area + Charred + Cover + Cuts + Diam. + Region + Standing/ha + Type	10	-210.583	441.4	2.70	0.024
Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Forest 2019 + Region + Standing/ha + Type	12	-208.640	441.6	2.89	0.022
Avg basal area + Charred + Continuity + Cover + Diam. + Fallen/ha + Region + Standing/ha + Type	11	-209.668	441.6	2.90	0.022
Charred + Continuity + Cover + Diam. + Forest 1960 + Region + Standing/ha + Type	10	-210.697	441.6	2.92	0.022
Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Forest 1960 + Region + Standing/ha + Type	12	-208.661	441.6	2.93	0.021
Avg basal area + Charred + Continuity + Cover + Diam. + Forest 2019 + Region + Standing/ha + Type	11	-209.721	441.7	3.01	0.021
Charred + Continuity + Cover + Cuts + Decay + Diam. + Fallen/ha + Region + Standing/ha + Type	12	-208.702	441.7	3.01	0.021
Charred + Continuity + Cover + Decay + Diam. + Region + Standing/ha + Type	10	-210.770	441.7	3.07	0.020
Avg basal area + Charred + Continuity + Cover + Diam. + Forest 1960 + Region + Standing/ha + Type	11	-209.869	442.0	3.31	0.018
Avg basal area + Charred + Continuity + Cover + Decay + Diam. + Region + Standing/ha + Type	11	-209.925	442.1	3.42	0.017
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Forest 2019 + Region + Standing/ha + Type	13	-207.889	442.1	3.43	0.017
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Fallen/ha + Forest 1960 + Region + Standing/ha + Type	13	-207.932	442.2	3.52	0.016
Avg basal area + Charred + Continuity + Cover + Cuts + Decay + Diam. + Fallen/ha + Region + Standing/ha + Type	13	-207.960	442.2	3.58	0.016
Avg basal area + Charred + Continuity + Cuts + Diam. + Region + Standing/ha + Type	10	-211.091	442.4	3.71	0.015
Charred + Continuity + Cover + Cuts + Diam. + Forest 1960 + Forest 2019 + Region + Standing/ha + Type	12	-209.062	442.4	3.73	0.014
Charred + Continuity + Cover + Cuts + Decay + Diam. + Forest 2019 + Region + Standing/ha + Type	12	-209.120	442.5	3.85	0.014
Charred + Continuity + Cover + Cuts + Decay + Diam. + Forest 1960 + Region + Standing/ha + Type	12	-209.151	442.6	3.91	0.013
Charred + Continuity + Cover + Diam. + Fallen/ha + Forest 2019 + Region + Standing/ha + Type	11	-210.199	442.6	3.97	0.013
Avg basal area + Charred + Continuity + Cover + Cuts + Diam. + Forest 1960 + Forest 2019 + Region + Standing/ha + Type	13	-208.165	442.6	3.99	0.013

Component models included in the Cladonia GLMM model averaging (deltaAICc < 4). Stand included as random variable in all models. Parameters explained in table 2.

Model	df	logLik	AICc	delta AICc	weight
Charred + Cover + Cuts + Decay + Diam. + Standing/ha + Type	9	-293.011	604.2	0.00	0.131
Charred + Continuity + Cover + Cuts + Decay + Diam. + Standing/ha + Type	10	-292.155	604.5	0.32	0.111
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Standing/ha + Type	10	-292.780	605.8	1.57	0.060
Charred + Cover + Cuts + Decay + Diam. + Region + Standing/ha + Type	10	-292.840	605.9	1.69	0.056
Charred + Cover + Cuts + Decay + Diam. + Forest 1960 + Standing/ha + Type	10	-292.845	605.9	1.70	0.056
Charred + Cover + Cuts + Decay + Diam. + Fallen/ha + Standing/ha + Type	10	-292.999	606.2	2.01	0.048
Charred + Cover + Cuts + Decay + Diam. + Forest 2019 + Standing/ha + Type	10	-293.003	606.2	2.02	0.048
Avg basal area + Charred + Continuity + Cover + Cuts + Decay + Diam. + Standing/ha + Type	11	-292.004	606.2	2.06	0.047
Charred + Continuity + Cover + Cuts + Decay + Diam. + Forest 1960 + Standing/ha + Type	11	-292.095	606.4	2.24	0.043
Charred + Continuity + Cover + Cuts + Decay + Diam. + Region + Standing/ha + Type	11	-292.117	606.5	2.28	0.042
Charred + Continuity + Cover + Cuts + Decay + Diam. + Fallen/ha + Standing/ha + Type	11	-292.132	606.5	2.31	0.041
Charred + Continuity + Cover + Cuts + Decay + Diam. + Forest 2019 + Standing/ha + Type	11	-292.155	606.5	2.36	0.040
Charred + Continuity + Cover + Decay + Diam. + Standing/ha + Type	9	-294.407	607.0	2.79	0.032
Charred + Cover + Decay + Diam. + Standing/ha + Type	8	-295.453	607.0	2.85	0.031
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Forest 1960 + Standing/ha + Type	11	-292.641	607.5	3.33	0.025
Charred + Cover + Cuts + Decay + Diam. + Forest 1960 + Region + Standing/ha + Type	11	-292.649	607.5	3.35	0.025
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Region + Standing/ha + Type	11	-292.735	607.7	3.52	0.022
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Forest 2019 + Standing/ha + Type	11	-292.779	607.8	3.61	0.022
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Fallen/ha + Standing/ha + Type	11	-292.779	607.8	3.61	0.022
Charred + Cover + Cuts + Decay + Diam. + Fallen/ha + Forest 1960 + Standing/ha + Type	11	-292.832	607.9	3.71	0.020
Charred + Cover + Cuts + Decay + Diam. + Fallen/ha + Region + Standing/ha + Type	11	-292.839	607.9	3.73	0.020
Charred + Cover + Cuts + Decay + Diam. + Forest 2019 + Region + Standing/ha + Type	11	-292.839	607.9	3.73	0.020
Charred + Cover + Cuts + Decay + Diam. + Forest 1960 + Forest 2019 + Standing/ha + Type	11	-292.844	607.9	3.74	0.020
Avg basal area + Charred + Cover + Cuts + Decay + Diam. + Type	9	-294.945	608.0	3.87	0.019

Appendix 4

The model-averaged parameter estimates with 95 % confidence interval from the conditional average for the GLMM of Hertelidea occurrence. The scale at which the variable was measured for the significant parameters. Presented in order of strength of effect (estimate farthest from zero). Parameters explained in table 2.

Hertelidae			
Factor	Estimate	2.5 % CI	97.5 % CI
(Intercept)	-2.91	-3.582	-2.23
Charred	3.18	2.59	3.77
Standing pine DW	-2.15	-3.03	-1.27
Region (north)	-0.99	-1.66	-0.32
Type (standing)	-0.99	-1.77	-0.20
Cover	-0.91	-1.68	-0.14
Diam.	0.87	0.33	1.40
Cuts	0.67	-0.05	1.39
Continuity area amount	0.63	0.06	1.20
Average basal area	-0.49	-1.23	0.25
Fallen pine DW	0.31	-0.36	0.99
2019 habitat amount	0.13	-0.38	0.63
1960 habitat amount	0.11	-0.48	0.69
Decay stage	0.03	-0.73	0.78

The model-averaged parameter estimates with 95 % confidence interval from the conditional average for the GLMM of Cladonia occurrence. The scale at which the variable was measured for the significant parameters. Presented in order of strength of effect (estimate farthest from zero). Parameters explained in table 2.

Cladonia			
Factor	Estimate	2.5 % CI	97.5 % CI
(Intercept)	-1.96	-2.69	-1.23
Type (standing)	-3.25	-4.02	-2.48
Cover	-2.14	-2.84	-1.44
Standing pine DW	-1.82	-3.30	-0.34
Charred	1.63	0.99	2.27
Decay stage	1.24	0.65	1.82
Diameter	0.93	0.42	1.45
Cutmarks	0.77	0.08	1.45
Continuity area amount	0.59	-0.32	1.50
Average basal area	-0.43	-1.69	0.83
Region (north)	0.24	-0.77	1.25
1960 habitat amount	0.22	-0.60	1.03
Fallen pine DW	0.06	-0.96	1.09
2019 habitat amount	0.023	-0.83	0.88