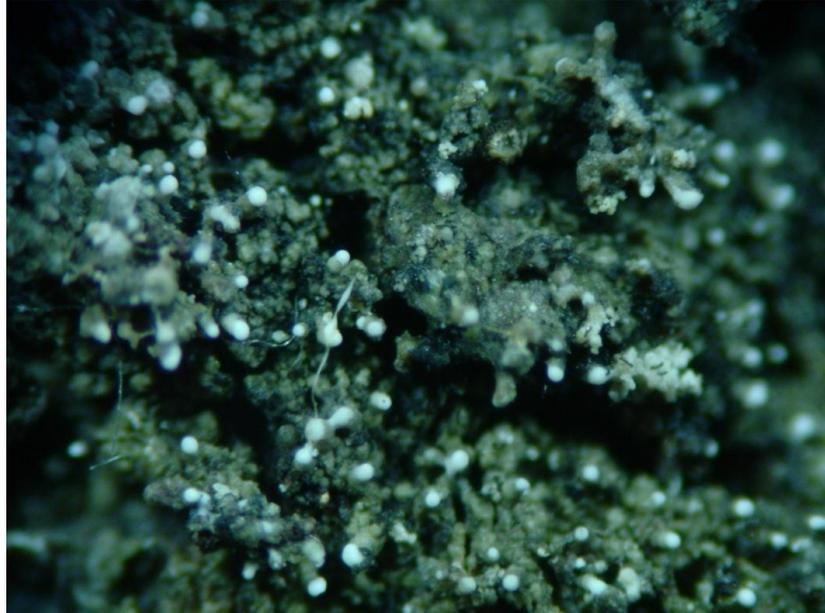




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The effects of forest age, forest edge and landscape factors on the occupancy and cover of the *Micarea globulosella* lichen in a Swedish boreal forest

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Abstract

Lichens are sensitive indicators of changes in environmental factors such as moisture, light intensity and air pollution. They are easily affected by forest fragmentation and by recent increases in forest edges as a result of intensive use of forest resources. The aim of this study was to describe previously unknown ecological characteristics of the *Micarea globulosella* lichen by (1) comparing the occupancy and cover of *M. globulosella* in old and young forest production stands, (2) investigating whether *M. globulosella* is affected by stand edges and (3) exploring the effect of high *M. globulosella* occupancy in old stands on lichen regeneration in young stands. The impacts of other landscape factors on *M. globulosella*, including altitude and latitude, were also tested. Most profoundly, *M. globulosella* was found in young forest stands. This contradicts current information which states that the lichen predominantly grows in old-growth forests with long tree continuity. Lichen occupancy and cover increased with stand age. *M. globulosella* responded to forest edges. In old South facing stands, there was a significant increase in occupancy with increasing distance from the stand edge towards the forest interior. In young North facing stands, lichen occupancy decreased significantly with increasing distance from the stand edge towards the forest interior of the young stand. In young South facing stands, contrary to expectations, there was a significant decrease in lichen occupancy with an increasing distance from the stand edge towards the forest interior of the young stand. A positive correlation between high lichen occupancy in old stands and increased lichen occupancy in the directly adjacent young stands was found. This study's findings suggest that *M. globulosella* regeneration and occupancy is affected by both microclimate and dispersal interactions.

Introduction

With the dawn of industrialised silviculture and intensive forest management for economic purposes and land use change, forests have become more fragmented over the past century. Forest fragmentation exposes forests to more weathering at the stand edges, with higher levels of solar radiation, greater temperature fluctuations, higher wind speeds and higher nitrogen deposition, i.e. edge effects (Chen et al. 1999; Esseen et al. 1997; Spangenberg & Kölling 2004). Forest fragmentation is considered one of the greatest threats to forest biodiversity (Esseen et al. 1997; Niemelä 1997), as many forest interior species require large areas of interior forest habitat, and are not adapted to changes in habitat found at recently created forest edges (Murcia 1995).

Among the species affected by forest fragmentation are lichens (Hazell & Gustafsson 1999). Lichens are excellent indicators of changes in their surrounding environments, as they are fragile and readily respond to changes in environmental conditions and microclimates (Coxson & Stevenson 2007; Nash III 2008). Lichens are symbiotic organisms that inhabit a great variety of terrestrial ecosystems, from the equator to Earth's polar regions and can grow on nearly all substrates. This symbiosis occurs between a fungus, the mycobiont, and a green alga or a cyanobacterium, the photobiont. Lichens are poikilohydric (lack mechanisms to regulate water uptake) and are highly dependent on atmospheric moisture, rain and other sources of water for growth, and are thus sensitive to microclimatic and environmental changes. They provide food and habitats for myriad insects, invertebrates, birds and mammals, affect the global nutrient cycle and greatly contribute to global biomass and biodiversity (Seaward 2008). Lichens play an essential role in Earth's ecosystems (Seaward 2008), but are threatened due to forestry operations and increasing forest fragmentation (Gustafsson et al. 2004; Rocío et al. 2007), air pollution (Jorund & Erlend 2008; Pisani et al. 2011) and reduced substrates (Spribille et al. 2008). Since the past decade, Scandinavian countries have developed legislation and

incentives for forest companies and owners to conserve biodiversity in the form of nature reserves, key habitats, forest retention zones, single-tree and high stump retention (Perhans et al. 2007 & 2009; Gustafsson & Perhans 2010). Several studies have shown that forest retention patches help stabilise lichen populations (Löhmus & Löhmus 2010) and provide substrates and some characteristics of old growth forests (Gustafsson et al. 2010). Despite forest retention patches other studies have shown that some species still respond negatively to increases in forest fragmentation and reduced amounts of old-growth structures (Perhans et al. 2007 & 2009; Gustafsson & Perhans 2010).

This study focuses on the crustose lichen species *Micarea globulosella* (Nyl.) Coppins, or the globe dot lichen, which was first described in 1983 (Santesson et al. 2004) but not previously studied regarding its ecology. *M. globulosella* has an approximately 0.4 mm wide greenish-grey coloured thallus and whitish-grey coloured pycnidia (Thor & Arvidsson 1999) and has an ascomycete mycobiont (USDA, last accessed 17. March, 2011). According to currently available knowledge, *M. globulosella* grows on bases of mature spruce and alder trees in moist forests and fens, signifies high air and soil moisture and long tree continuity, and is thought to efficiently disperse throughout the landscape possibly via thallus fragments and/or spores, though *M. globulosella* dispersal mechanisms remain unknown (Thor & Arvidsson 1999; Thor, G., *personal communication*). In 1999 *M. globulosella* was added to the Swedish Red List, which classifies the viability of protected and endangered species in Sweden (Thor & Arvidsson 1999), but after a survey conducted in boreal Sweden in 2002, the lichen was removed from the list as it was found to be highly common in production forests (Gustafsson et al. 2004; Rudolphi & Gustafsson 2011). *M. globulosella* is a crustose lichen, which means the entire lichen is tightly bound to its substrate surface and can only be removed via destruction of the thallus (Büdel & Scheidegger 2008). Water loss occurs primarily at the upper, exposed surface and this lichen type benefits from water flow across the substrate surface. Crustose

lichens can successfully tolerate and grow in extreme sites, including bare rock surfaces (Büdel & Scheidegger 2008).

In this current study, I used data from a survey of 19 old and young forest stands conducted in 2003 and 2004 to explore the ecological characteristics of the *M. globulosella* lichen.

Literature review

This literature review investigates findings from ecological studies of lichen species. The aim is to introduce the background principles and theories of lichen responses to edge effects, lichen life cycle and dispersal. This study's hypotheses and research questions are based upon the principles of previous findings introduced in this literature review.

Ecological studies on lichens

There are a number of studies that investigate and discuss whether fruticose, pendulous or foliose lichens show a response (i.e. change in occurrence, growth and dispersal) when growing close to a forest edge. Fruticose pendulous lichens have highly branched, hair-like thalli and protrude from the substrate surface. Foliose lichens are leaf-like and flat in shape and are also only partially attached to their substrate surface (Büdel & Scheidegger 2008). Kivistö & Kuusinen (2000) conducted a survey on epiphytic lichen species and showed that lichen diversity was lower at the forest edge with a South (S) orientation, while there was no species diversity gradient on North (N) facing edges. In this case, the authors argued that a less hospitable microclimate for poikilohydric lichens on the S-facing edges resulted in lower species richness, than on N-facing edges where a more stable microclimate exists.

In support of Kivistö & Kuusinen (2000), Hylander (2005) found that the two pleurocarp bryophytes, *Hylocomium splendens* and *Hylocomiastrum umbratum* showed lower growth rates at S facing edges than at N facing edges due to a drier microclimate at the S-facing edges. Despite the fact that Hylander (2005) studies two moss species, the results are still relevant as both mosses and lichens are poikilohydric.

In more species specific studies, Renhorn et al. (1997) investigated the two foliose lichen species, *Platismatica glauca* and *Lobaria pulmonaria* and did not observe a change in growth closer to the forest edge. This contrasts previously mentioned studies. In fact, the highest growth was observed 12 m from the forest edge. This may be attributable to the following factors. Firstly, in the forest Renhorn et al. conducted their study, only small differences in temperatures and humidity were observed at forest edges versus in the interior. With the combination of little measurable change in temperature and a 4.3 times higher solar radiation level near the forest edge compared to the interior, the authors suggest that these factors may have contributed to the high lichen growth measured at the forest edge. In another study, Esseen & Renhorn (1998) studied the pendulous lichen species, *Alectoria sarmentosa* which showed a reduced growth rate close to the forest edge. The authors suggest that the main cause for the decline in growth rates closer to the edge was physical damage to the fragile pendulous lichen thallus by wind. Furthermore, in concurrence with Renhorn et al. (1997), Esseen and Renhorn (1998) observed the highest growth 20-30 m from the forest edge, where irradiance was a factor hypothesised to influence the high thallus growth rates. Hilmo & Holien (2002) compared a variety of foliose, crustose and pendulous lichens and their growth at forest edges. Results showed strong species specific responses, with the strongest forest edge effects (i.e. lowest lichen cover near the forest edge) on foliose lichens, and the weakest edge effects (i.e. least reduction in cover near the forest edge) in crustose lichens. The observed weak response of crustose lichens to forest edges may be due to crustose lichens possessing a higher

resilience to a variety of microclimatic conditions (Hilmo & Holien 2002). Jansson et al. (2009) studied the pendulous lichen, *Usnea longissima*. Close to the forest edge they observed a weight gain in long lichen thalli, however not in short thalli. Further into the forest growth rates and edge effects declined. Highest chlorophyll α levels and growth increases were found close to the forest edge, probably due to higher irradiance near the forest edge.

In order to study the edge effects in a non-anthropogenically altered environment, Moen & Jonsson (2003) investigated the influence of shapes and sizes of forested islands on lichens in a boreal wetland. Results were strongly species specific. The *Microcalicium disseminatum* lichen showed a nearly two times higher occurrence on large islands than on small islands, while the hepatic *Lophozia silvicola* showed a 1.6 times higher occurrence on large than on small islands. Overall, Moen & Jonsson found a greater frequency, cover and species diversity of hepatics (liverworts) and lichens in larger and rounder forest islands between 4-6 ha in size than in smaller and irregular shaped islands less than 1 ha in size. This may be due to forest structures assuming more interior characteristics in circular forested islands than in irregular shaped or smaller islands.

There are few studies on dispersal and regeneration of lichen populations in relation to stand edges. Dettki et al. (2000) researched whether lichens growing in old-growth stands (122 – 298 years old) had any impact on lichen regeneration in adjacent young stands (35 – 78 years old), i.e. propagule effect. Dettki et al. found a significant decrease in both foliose and pendulous fruticose lichen thalli with increasing distance away from the old-growth forest. Several epiphytic lichen species were tested. The pendulous *Bryoria* spp. and foliose *Hypogymnia* spp. lichens showed close to 50% reduction in thallus numbers 100 m from the edge of the old-growth forest, compared to the number of thalli found 10 m from the forest edge. According to Dettki et al., the observed reduction in thalli may have been due to a lower availability of dispersed thallus fragments further away from the

propagule source, i.e. reduced propagule numbers further away from the propagule source. In contrast, Hylander (2009) studied the effect of propagule sources on 21 bryophyte species and observed no increases in colonisation rates closer to the propagule source. This may have been due to a high background source of propagules.

Lichen life cycle

There are five stages of a lichen's life cycle: (1) propagule attachment, (2) germination, (3) growth, (4) reproduction and (5) dispersal (Armstrong 1988). Lichens reproduce sexually via mycobiont spores or asexually via thallus fragments, soredia, isidia or hormocysts. Asexual lichen reproduction implies that the propagules are already symbiotic (Bowler & Rundel 1975; Bailey 1976). While most lichens possess a type of asexual reproduction, both sexual and asexual reproduction is possible on one species. How efficiently various types of lichen propagules disperse is still unknown (Armstrong 1988). Studies have shown that lichens show species specific responses to forestry operations. This may be due to variations in the efficiency of propagule dispersal among lichen species (Esseen et al. 1996; Peck & McCune 1997). Green-algal foliose lichens have been observed to rapidly colonise young forests via the production of myriad miniature propagules which consist of soredia. On the other hand, pendulous lichens have shown to colonise forests more slowly. This is probably a result of larger propagules, i.e. thallus fragments impacting dispersal (Dettki 1998).

Scope, aims of study and hypotheses

In this study I statistically analysed data that was collected in a survey designed by Rudolphi and Gustafsson in Hälsingland, Sweden in 2003. Collected data in the *Micarea globulosella* lichen had not yet been evaluated.

The aims of this study were to (1) compare the occupancy and cover of *M. globulosella* in old and young forest production stands, (2) investigate whether *M. globulosella* is affected by stand edges (3) explore if the lichen occupancy and cover in young forest is affected by a high occupancy in the adjacent old stands, (4) explore if *M. globulosella* has a higher occupancy and cover closer to bodies of water and wetlands, (5) examine whether altitude and (7) latitude and longitude play a role in *M. globulosella* occupancy and cover.

I hypothesised that (1) *M. globulosella* has a higher occupancy and cover in an old forest than a young forest since the lichen has more time to establish itself in an old forest, (2) there will be a higher *M. globulosella* occupancy and cover on North facing edges of old stands and lower occupancy and cover on South facing edges of young stands due to more favourable microclimatic conditions for growth at N-facing aspects, including lower average temperatures, lower evaporation rates and higher humidity, (3) *M. globulosella* will have a higher occurrence closer to the propagule source, the old stand, (4) *M. globulosella* occupancy and cover will be highest close to open water and wetlands and lowest far away from water and wetlands since closer to a source of moisture the microclimate may be more humid and thus more favourable for growth, (5) lichen occupancy and cover will be highest in areas surrounded by the largest area of water bodies, (6) *M. globulosella* occupancy and cover will be greater at higher (maximum 390 m) than at lower (minimum 120 m) elevations and (7)

at higher latitudes due to a moister and cooler microclimate and a historically lower impact of silviculture at higher elevations and latitudes.

Apart from Hilmo & Holien (2002) there are very few ecological studies on crustose lichens and no studies on *M. globulosella*. In addition, there are very few paired studies in which the ecology and growth of lichens in both young and old forest stands and the respective stand edges are investigated (Murcia 1995; Fonseca & Joner 2007). In my case the young forest stand was located at one side of the edge, while the old forest was on the other side. I also aimed to increase the amount of information available on the still newly discovered lichen species *M. globulosella*, which was first described by Brian Coppins in 1983 (Santesson et al. 2004). Finally, I provide new photographic material on *M. globulosella*.

Materials and methods

Study site and species inventory

Rudolphi and Gustafsson (R. & G.) conducted a survey of red-listed species in young and old forest stands with lichens recorded during the summer of 2003, and bryophytes recorded during the summer of 2004. The study site was located in a 4,700 km² area in Gävleborg County in central Sweden. The forest company Holmen Skog owns the forest land R. & G. conducted their survey on. The centre point of their research area lies at 61°57'N, 16°30'E, in the boundary zone between the southern and middle boreal vegetation zones (Ahti et al. 1968). Stands were Norway Spruce (*Picea abies* L. Karsten) dominated, mixed with a limited number of deciduous tree species, including birch (*Betula* spp.), alder (*Alnus* spp.), aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.) and willow

(*Salix* spp.) (Rudolphi & Gustafsson 2011). Rolling hills made up the topography of the area. The highest elevation was 390 m, while the lowest elevation was 120 m.

R. & G. studied the stand database from Holmen Skog prior to the field survey, and selected sites that were larger than 3 ha in size and situated on land less than 400 m above sea level. The research plots consisted of tree stands directly opposite to each other (i.e. old stands facing young stands divided by a stand edge) and of two age groups: 1) young even-aged stands with trees of 30-70 years of age with a varying stand age between young plots and 2) old stands of 95-125 years of age, with a varying stand age between old plots. Each plot, old and young, has a certain and individual stand age. R. & G. divided the land into a total of 19 stand pairs of 100 m x 100 m plots along the boundary line between the young and old forest stands. Due to topographic disturbances (i.e. streams, logging roads, partial cuttings, etc.), R. & G. made small adjustments in order to ensure equal plot sizes. Ideally, the total area of all study plots for young and old forest, respectively, should have amounted to 19 ha in size, but due to uneven plot borders and oblique angles between plots, the area totalled 17.7 ha for each age class. While old forest stands probably had never been cut, the young stands were even-aged and had been previously clear-cut and replanted with *P. abies*. According to the stand data base of the forest company the age of the old forest was based on the age of the dominating tree layer, while the young forest age corresponded to actual stand age (Rudolphi & Gustafsson 2011).

Production stands are designated for timber production according to the long-term planning of the forest owner. According to current Swedish forestry practices, they will eventually be clear-cut. Most of the old stands in the current study had management actions including thinning, but some were only slightly affected by forest operations. Despite some management actions, there were legacies of a former natural forest landscape, with considerable quantities of old-growth structures such as old

trees and dead wood. It is very hard to accurately date such old stands which may have had varying levels of tree continuity over the centuries, and thus the age according to the forest company stand data bases is often a large underestimation. On the other hand, young forest stands regenerating after a clear-cut can be accurately dated as they are even-aged.

I used data from the following survey. As part of an extensive survey on red-listed lichens in 2003, *Micarea globulosella* presence was investigated in a separate sub-study, but this data has so far not been analysed or published. Transects were mapped out running perpendicular to the centre of the edge between the young and old stands. Circular test subplots with a 5 m radius were established along the transect lines at distances of 5 m, 20 m, 40 m, 60 m and 80 m from the stand edges (Figure 1). The aspect of old and young test plots depended on the aspect of the stand edge. No efforts were made to select specific aspects.

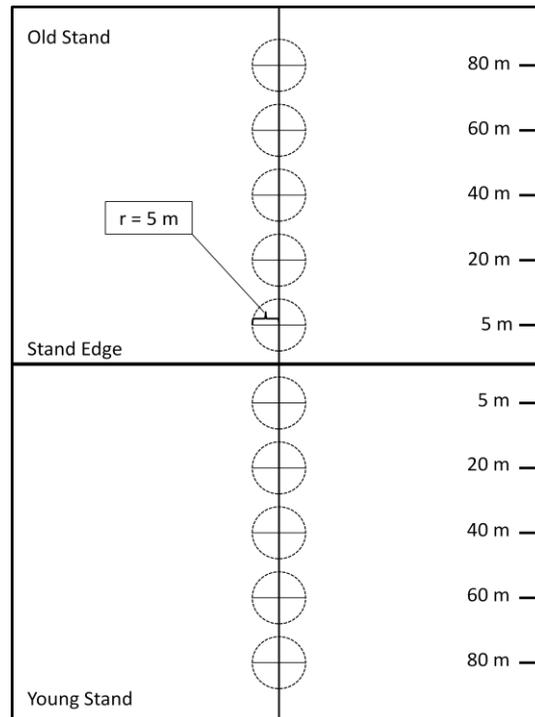


Figure 1. Experimental design of the *Micarea globulosella* lichen survey. Young and old forest stands were opposite to each other with a common stand edge. At 5 m, 20 m, 40 m, 60 m and 80 m test sub plots were established with a 5 m radius. Old and young stand plots were, respectively, 100 m x 100 m in size. Stand edges always faced old and young forest plots, and were not intersected by clear-cuts, water, or other land forms.

The 5 closest possible host trees, *P. abies* or *Betula spp.*, with a greater or equal diameter at breast height of 10 cm were located and surveyed for the *M. globulosella* lichen. Occupancy measured the number of trees out of 5 that hosted *M. globulosella* on their trunks. In addition, lichen cover was also investigated on the 5 host trees. A three-step scale was used to measure this: 0 = 0 cm², 1 < 10 cm², 2 > 10-400 cm² and 3 > 400 cm² lichen cover on tree trunks. All trees were surveyed to a trunk height of 2 m.

Landscape variables

I considered the landscape variables elevation, vicinity and area of water bodies, vicinity of wetlands, latitude and longitude, and edge aspect as potentially important for *Micarea globulosella* occurrence

in old as well as young stands. In addition, I considered the area of old forest surrounding the young plots, and the sum of trees occupied by *M. globulosella* in the old plots as potentially important for *M. globulosella* regeneration (i.e. occupancy) in the young stands. I presume that both the area of old forest surrounding the young plots, as well as lichen occupancy in the old plots, is a proxy of the size of the propagule source. R. & G. extracted altitude information from the Holmen forest company stand database. I uploaded the locations of every test subplot in old and young stands onto ArcMap (ESRI. Environmental Systems Resource Institute. 2009. ArcGIS 9.2. ESRI, Redlands, California). To measure the vicinity and area of water bodies and the vicinity of wetlands I mapped the centre point of each edge between young and old stands in ArcMap using the Midpoint Tool. I calculated the distances from edge centres to closest open bodies of water and wetlands, respectively, with a minimum size of 0.1 ha, and within a distance of 1,000 m. Due to lack of open water bodies within this distance, consequently, I changed the criterion for this variable to embrace closest occurrence of open water, irrespective of distance. This implied that the largest distance was 2,217 m. On the other hand, I could successfully carry out wetland Near (i.e. how close wetlands were to the stand edges) calculations with values for all stands using the 1,000 m criterion. I calculated the area of water bodies using the edge midpoints mentioned above and the ArcMap Buffer and Clip Tools. I established 300 m and 1,000 m buffer zones, respectively, around the edge centre points in ArcMap. I computed water body area values using the Clip Tool. I obtained latitude and longitude data from the analyses of R. & G.. I extracted data on edge aspect from ArcMap using the edge midpoints and the directional data of the test subplots in each stand pair. I classified old and young stands into two cardinal directions (i.e. direction on a compass). I designated East (E), Northeast (NE), North (N) and Northwest (NW) facing stands as "North" (n=9), while West (W), Southwest (SW), South (S) and Southeast (SE) facing slopes as "South" (n=10). Merging cardinal directions into N and S simplified calculations. I combined E, NE, N and NW based on the assumption that forest stand edges with these orientations receive the lowest solar radiation and possess the coolest microclimates on average. W, SW, S and SE receive the highest solar radiation levels and the highest temperatures

(Moseley et al. 2009; Matlack 1993; Chen et al. 1995; Hylander 2005, Rudolphi & Gustafsson personal communication). To measure the quantity of old forest surrounding the young forest stands, I extracted data from 2 virtual buffer zones reaching 100 m and 1,000 m from the edge of the young plots, as done by Rudolphi & Gustafsson (2011). R. & G. quantitatively assessed the area of old forest that was present within each individual buffer zone in ha using k-Nearest Neighbour satellite mapping, with a 25 m x 25 m resolution (Reese et al. 2003). Finally, I calculated the sum of the trees occupied by *M. globulosella* in the old test plots to investigate whether a high *M. globulosella* occupancy in the old plots affected lichen regeneration in the young plots.

Statistical analysis

Stands number 20, 21 and 23 had higher values for occupancy and cover than the rest of the stands and they were located further S than the rest of the test stands. Hence these three stands were outliers. Due to the fact that I aimed for more homogeneous plots in terms of occupancy, cover and location, I omitted the three outlier stands. Despite this, I conducted two sets of tests, one with n = 19 and a second with n = 16, respectively to test whether and how these three outliers would affect the results.

Micarea globulosella occupancy

To investigate if *Micarea globulosella* occupancy was higher on North and/or South aspects and in young and/or old stands, I tested my hypotheses using a Generalised Linear Model (GLM) and separated the data into, i) N-young ii) S-young iii) N-old and iv) S-old. N-young represented young stands with N facing stand edges, S-young represented young stands with S facing stand edges, N-old corresponded to old stands with N facing stand edges and S-old corresponded to old stands with S facing edges. In addition, I executed detailed GLM's where the effects of the co-variables: i) distance to stand edge (Distance), ii) stand age (Age), iii) stand elevation (Elevation), iv) area of water within a

300 m and 1000 m virtual buffer zone (H₂O 300 and H₂O 1000), v) latitude, vi) longitude, vii) stand edges to open water bodies (Distance Water), viii) stand edges to wetlands within a 1,000 m radius (Distance Wetlands), ix) area of old forest within 100 m and 1,000 m from the young plots (Old Forest 100 and Old Forest 1,000) and x) sum of occupied trees in adjoining old stand (Sum Occupancy in Old) on *M. globulosella* occupancy were all included in the GLM model. Abbreviated names of the co-variables are in parentheses and I will use them in this form throughout the rest of the paper for clarity purposes. I ran another GLM model to investigate if *M. globulosella* occupancy in young stands changed when moving away from the old forest stands towards the interior of the young stands. With this test I aimed to detect any possible effects the assumed propagule source, i.e. the old stand, may have on the regenerating *M. globulosella* population in the young stands. I used stepwise Akaike's Information Criterion (AIC) to simplify my models.

***Micarea globulosella* cover**

I used the Wilcoxon rank sum test to investigate if *Micarea globulosella* cover was affected by stand age. I used Ordinal Logistic Regression (OLR), as recommended by Chatterjee et al. (2006), to test if the distance from stand edge and edge aspect affected lichen cover. I executed detailed ordinal logistic regression (OLR) analyses including all the previously mentioned 10 co-variables. When analysing all data in GLMs and OLRs I noticed three outliers, stands 20, 21 and 23. In order to investigate whether the outlier stands had a strong impact on my results, I ran all Wilcoxon rank sum tests, GLMs and OLRs for both n = 19 and n = 16 scenarios.

Finally, I visually evaluated graphs showing occupancy and cover in the young and old forest stands. I carried out all statistical analyses in R statistical software (R Foundation for Statistical Computing,

Version 2.12.2, Vienna, Austria. 2011), using the “Design” package to calculate OLR’s (Design: Design Package. R Package Version 2.3-0).

Results

Stand characteristics

The following results are for n = 19. According to the Holmen Skog forest company stand database, the mean age of young and old stands was significantly different (t-test, $p < 0.001$). There was no significant difference in the mean percentage of *P. abies* between the young and old stands (t-test, $p = 0.202$), of *P. sylvestris* (t-test, $p = 0.399$), and of deciduous trees (t-test, $p = 0.266$) in young and old stands, respectively. Site index, ground moisture class, ground surface structure and elevation were very similar in young and old stands (Table 1).

For n = 16 mean stand age, mean percentage *P. abies*, *P. sylvestris* and deciduous trees, site index, ground moisture class, ground surface structure and elevation were very similar to n = 19 (Table 1).

Table 1. Stand characteristics of the test stands for n = 19 and n = 16, respectively. Stand information for n = 19 and n = 16 is very similar. Means and standard errors are given.

	Young stands; n = 19	Old stands; n = 19	Young stands; n = 16	Old stands; n = 16
Mean Age (years) ± SE	44.3 ± 3.1	104.8 ± 2.1	42.9 ± 3.4	103.2 ± 2.0
Mean Elevation (m) ± SE	285 ± 18.3	286 ± 18.9	283 ± 21.3	280 ± 21.9
Mean Percentage <i>Picea abies</i> ± SE	72.4 ± 2.8	75.8 ± 2.9	72.7 ± 3.0	75.0 ± 3.0
Mean Percentage <i>Pinus sylvestris</i> ± SE	14.3 ± 2.8	13.4 ± 2.4	12.9 ± 3.0	12.1 ± 2.3
Mean Percentage <i>Deciduous Trees</i> ± SE	13.3 ± 3.0	10.8 ± 2.8	14.4 ± 3.5	12.9 ± 3.1
Site Index (n stands) ^b	G20 (3); G21 (1); G22 (4); G23 (5); G24 (2); G25 (1); G26 (2); T22(1)	G20 (3); G21 (4); G22 (3); G23 (3); G24 (3); G26 (3)	G20 (2); G21 (1); G22 (4); G23 (4); G24 (1); G25 (1); G26 (2); T22(1)	G20 (3); G21 (4); G22 (2); G23 (3); G24 (2); G26 (2)
Ground Moisture Class (n stands) ^c	Mesic (16); Moist (3)	Mesic (16); Moist (3)	Mesic (16); Moist (3)	Mesic (16); Moist (3)
Ground Surface Structure (n stands) ^d	Even (16); Somewhat Uneven (3)	Very Even (1); Even (16); Somewhat Uneven (2)	Even (13); Somewhat Uneven (3)	Very Even (1); Even (13); Somewhat Uneven (2)

^aStand information was extracted from the Holmen Skog forest company database. Table structure was adopted from Rudolphi & Gustafsson (2011).

^bDominant tree height at total age of 100 years. Measure used to evaluate site quality (Hägglund & Lundmark 1977).

^cMeasure of soil water content based on average depth of groundwater table during the growing season (MarkInfo).

^dMeasure of ground evenness and slope (Skogforsk).

Landscape characteristics

The following results, including means and standard errors are for n = 19. The mean area of water within a 300 m buffer was 0.2 ± 0.04 ha and for a 1,000 m buffer 4.5 ± 1.2 ha. The mean distance to the closest wetland within a 1,000 m radius was 196.6 ± 11.7 m. The mean distance to the closest open water body was relatively far at 1034.9 ± 62.15 m from the stand edges. There was relatively little old forest when considering a 100 m buffer at 3.5 ± 0.36 ha, whereas with a 1,000 m buffer there were 194.9 ± 8.46 ha of old forest surrounding young plots. (Table 2).

For n = 16, mean area of water within 300 m and 1,000 m from the centre point of the stand edges, mean distance to the closest wetland within 1,000 m, mean distance to open water bodies and area of old forest surrounding the young stands were very similar to the values in n = 19. Values for landscape characteristics for young and old stands were identical, as all landscape distance and area

measurements had a common centre point, namely directly at the centre point of the stand edge between the old and young stands (Table 2).

Table 2. Landscape characteristics of test plots for n = 19 and n = 16. Means and standard errors are given.

	All stands; n = 19 ^{a,b}	All stands; n = 16 ^{a,b}
Mean water within 300 m virtual buffer ± SE (ha)	0.2 ± 0.04	0.2 ± 0.05
Mean water within 1000 m virtual buffer ± SE (ha)	4.5 ± 1.20	5.3 ± 1.41
Mean distance to closest wetland within 1000 m radius (m)	196.6 ± 11.17	198.7 ± 13.20
Mean distance to closest open water body ± SE (m)	1034.9 ± 62.15	975.4 ± 71.74
Mean area of old forest within 100 m virtual buffer ± SE (ha)	3.5 ± 0.36	3.6 ± 0.18
Mean area of old forest within 1000 m virtual buffer ± SE (ha)	194.9 ± 8.46	194.3 ± 4.25

^aLandscape information was extracted from the Holmen Skog forest company database. ArcMap buffers were originally calculated by J. Rudolphi.
^bYoung and old stands were not considered separately as identical values for both would have made this table redundant

***Micarea globulosella* occupancy and cover – young stands**

The mean number of trees occupied by *Micarea globulosella* in the young stands out of a maximum occupancy value of 5 was 0.632 ± 0.123 for n = 19, and 0.338 ± 0.071 for n = 16, respectively. The mean lichen cover out of a maximum cover value of 3 was 0.421 ± 0.070 for n = 19, and 0.288 ± 0.038 for n = 16 stands, respectively. Figure 2 and Figure 3 visually depict mean *M. globulosella* occupancies at various distances from the stand edge for n = 19 and n = 16, respectively.

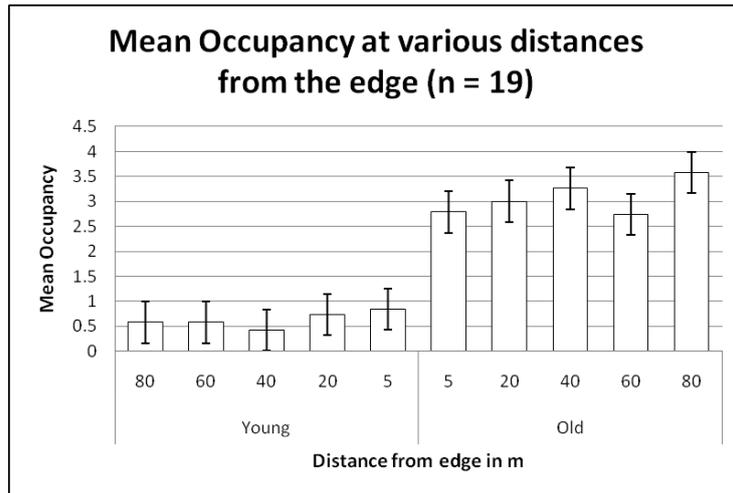


Figure 2. Mean *Micarea globulosella* occupancy values (number of trees out of 5 occupied by *M. globulosella*) in young and old stands at various distances from the stand edge for n = 19. Distances 5 m, 20 m, 40 m, 60 m and 80 m represent the test subplots and their distances from the stand edge. The error bars represent standard error and are shown for every distance.

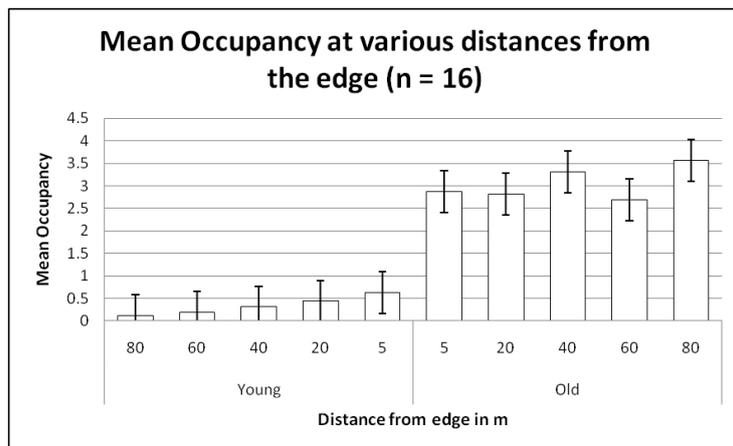


Figure 3. Mean *Micarea globulosella* occupancy values (number of trees out of 5 occupied by *M. globulosella*) in young and old stands at various distances from the stand edge for n = 16. Distances 5 m, 20 m, 40 m, 60 m and 80 m represent the test subplots and their distances from the stand edge. The error bars represent standard error and are shown for every distance.

Mean *M. globulosella* occupancy differed significantly between young and old forest stands (Wilcoxon rank sum test, $p < 0.001$, $n=19$), with lower mean lichen occupancy in the young stands compared to old stands. The same observation was made for $n = 16$. Median *M. globulosella* occupancy was 4 out of 5 possible trees in old stands, and 0 out of 5 possible trees in the young

stands for n = 19. Three outliers were present in n = 19, at the values 3, 4 and 5 out of 5 possible trees. The three outliers affected the results of the models and of Figures 2 and 3 due to a positive skew (Figure 4).

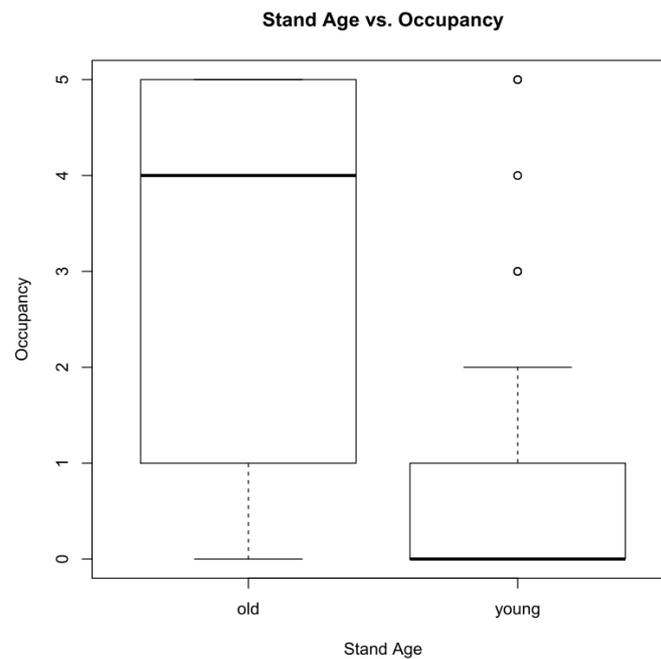


Figure 4. Median *Micarea globulosella* occupancy in young and old stands for n = 19. Very similar observations were made in n = 16 and a figure describing n = 16 would have been redundant. The boxes represent the middle 50 % of the data. The thick black horizontal lines in the boxes represent the median lichen occupancy values in young and old stands. Whiskers represent the minimum and maximum values at 1.5 of the interquartile range below the 25th percentile for old and above the 75th percentile for young stands, respectively. Outliers are represented by three dots above the box representing young stands.

Lichen occupancy increased significantly with stand age in young stands in both n = 19 (Table 3) and n = 16 (Table 4).

Table 3. GLM analysis for *Micarea globulosella* occupancy for n = 19. Significant values are highlighted in bold. Estimates indicate a negative or positive direction of the effect.

	Young stands; n = 19		Old stands; n = 19	
	Estimate	P-value	Estimate	P-value
Distance to stand edge (m)	-0.009	0.137	0.008	0.057
Stand age (years)	0.086	< 0.001	0.038	0.009
Stand elevation (m)	0.007	0.142	0.004	0.122
Water area (ha) within 300 m / 1000 m virtual buffer	n.a. ^a / n.a. ^a	n.a. ^a / n.a. ^a	1.191 / n.a. ^a	0.003 / n.a. ^a
Latitude (x-coordinate)	< -0.001	< 0.001	< 0.001	< 0.001
Longitude (y-coordinate)	n.a. ^a	n.a. ^a	n.a. ^a	n.a. ^a
Near calculation: stand edges to open water bodies	n.a. ^a	n.a. ^a	0.002	< 0.001
Near calculation: stand edges to wetlands within 1000 m radius	-0.006	0.041	-0.001	0.409
Area old forest within 100 m buffer centred in young forest stands	n.a. ^a	n.a. ^a	n.a. ^a	n.a. ^a
Area old forest within 1000 m buffer centred in young forest stands	-0.012	0.145	n.a. ^a	n.a. ^a
Number of trees occupied by <i>M. globulosella</i> in old stands	0.145	0.001	n.a. ^a	n.a. ^a

^a Co-variable was eliminated from calculations via AIC

Table 4. GLM analysis for *Micarea globulosella* occupancy for n = 16. Outlier stands number 20, 21 and 23 were omitted from this test. Significant values are highlighted in bold. Estimates indicate a negative or positive direction of the effect. Note the changes in significances from n = 19.

	Young stands; n = 16		Old stands; n = 16	
	Estimate	P-value	Estimate	P-value
Distance to stand edge (m)	-0.024	0.006	0.010	0.052
Stand age (years)	0.061	0.013	0.128	< 0.001
Stand elevation (m)	-0.884	0.196	0.013	< 0.001
Water area (ha) within 300 m / 1000 m virtual buffer	-0.005 / n.a. ^a	0.043 / n.a. ^a	2.919 / n.a. ^a	< 0.001 / n.a. ^a
Latitude (x-coordinate)	n.a. ^a	n.a. ^a	n.a. ^a	n.a. ^a
Longitude (y-coordinate)	n.a. ^a	n.a. ^a	< 0.001	< 0.001
Near calculation: stand edges to open water bodies	n.a. ^a	n.a. ^a	0.003	< 0.001
Near calculation: stand edges to wetlands within 1000 m radius	n.a. ^a	n.a. ^a	n.a. ^a	n.a. ^a
Area old forest within 100 m buffer centred in young forest stands	n.a. ^a	n.a. ^a	n.a. ^a	n.a. ^a
Area old forest within 1000 m buffer centred in young forest stands	-0.014	0.089	0.031	< 0.001
Number of trees occupied by <i>M. globulosella</i> in old stands	0.090	0.021	n.a. ^a	n.a. ^a

^a Co-variable was eliminated from calculations via AIC

Mean *M. globulosella* cover differed significantly between young and old forest stands (Wilcoxon rank sum test, $p < 0.001$), with lower mean lichen cover in the young stands compared to old stands. One outlier is present, with a cover value of 3, which represents a lichen cover of greater than 400 cm^2 on the three-step cover scale (Figure 5).

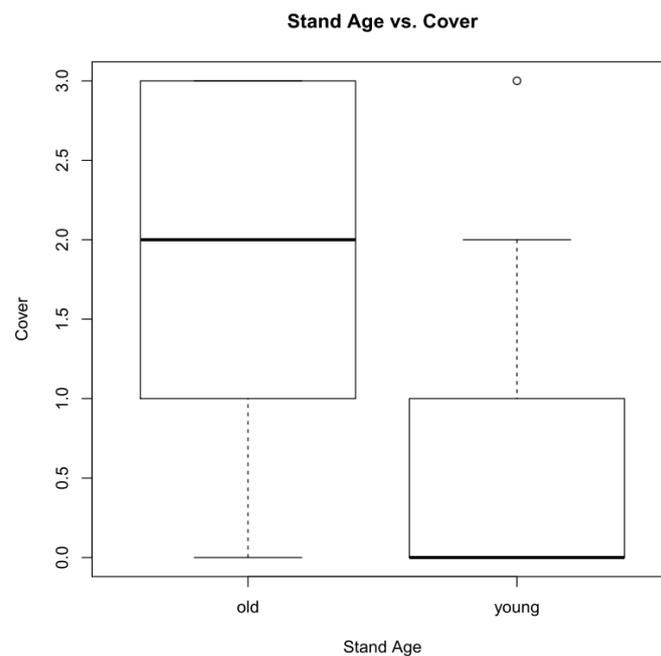


Figure 5. Median *Micarea globulosella* cover in young and old stands for $n = 19$. Very similar observations were made in $n = 16$ and a figure describing $n = 16$ would have been redundant. The boxes represent the middle 50 % of the data. The thick black horizontal lines in the boxes represent the median lichen occupancy values in young and old stands. Whiskers represent the minimum and maximum values at 1.5 of the interquartile range below the 25th percentile for old and above the 75th percentile for young stands, respectively. An outlier is represented by a dot above the box representing young stands.

The following results are for $n = 19$. Most of the test subplots in the young stands showed a cover value of 0, which represents 0 cm^2 lichen cover on the three-step cover scale. Between 10.5 % and 36.8 % of test plots had a cover value of 1, which represents less than 10 cm^2 lichen cover on the three-step cover scale. Only between 5.3 % and 10.5 % of the test subplots showed a cover value of 2

(10 – 400 cm² cover), and 0 % of the test plots showed the highest cover value of 3 (greater than 400 cm² lichen cover). (Table 5).

For n = 16, most of the trees found in the young test subplots showed *M. globulosella* cover values of 0, while around 12.5 % to 37.5 % showed a cover value of 1. Few test subplots showed a cover value of 2, and 0% of the test subplots in the young stands showed a cover value of 3. Lichen cover was relatively uniform in the old stands, with more similar percentages of trees with cover values of 0 – 3 than in the young stands. In old stands more trees showed cover values of 2 and 3, compared to the young stands (Table 5).

Table 5. Mean *Micarea globulosella* occupancy and cover ± SE at various test subplot distances from the stand edges. Table shows results for young and old stands with n = 19 and n = 16. A three step cover code scale is used to quantify cover on trees. Most trees observed with lichen cover values between 0 and 2 were found in young stands, while the cover values of 2 and 3 are more common in the old stands. This pattern can be observed for n = 19 and n = 16.

		Young Stands (n = 19)				Old Stands (n = 19)				
Distance from Edge (m)	Mean Occupancy out of 5 ± SE	Cover (%) ^a				Mean Occupancy out of 5 ± SE	Cover (%) ^a			
5	0.842 ± 0.318	0: 63.2	1: 21.1	2: 10.5	3: 5.3	2.789 ± 0.475	0: 26.3	1: 15.8	2: 21.1	3: 36.8
20	0.737 ± 0.263	0: 57.9	1: 36.8	2: 5.3	3: 0.0	3.000 ± 0.452	0: 21.1	1: 21.1	2: 26.3	3: 31.6
40	0.421 ± 0.299	0: 63.2	1: 36.8	2: 0.0	3: 0.0	3.263 ± 0.425	0: 5.3	1: 26.3	2: 21.1	3: 47.4
60	0.579 ± 0.299	0: 73.7	1: 15.8	2: 10.5	3: 0.0	2.7368 ± 0.451	0: 21.1	1: 21.1	2: 36.8	3: 21.1
80	0.579 ± 0.327	0: 78.9	1: 10.5	2: 10.5	3: 0.0	3.579 ± 0.345	0: 5.3	1: 21.1	2: 31.6	3: 42.1
		Young Stands (n = 16)				Old Stands (n = 16)				
Distance from Edge (m)	Mean Occupancy out of 5 ± SE	Cover (%) ^a				Mean Occupancy out of 5 ± SE	Cover (%) ^a			
5	0.625 ± 0.256	0: 68.8	1: 18.8	2: 12.5	3: 0.0	2.875 ± 0.531	0: 25.0	1: 18.8	2: 18.8	3: 37.5
20	0.438 ± 0.157	0: 62.5	1: 37.5	2: 0.0	3: 0.0	2.813 ± 0.502	0: 25.0	1: 25.0	2: 12.5	3: 37.5
40	0.313 ± 0.120	0: 68.8	1: 31.3	2: 0.0	3: 0.0	3.313 ± 0.481	0: 6.3	1: 25.0	2: 12.5	3: 56.3
60	0.188 ± 0.101	0: 81.3	1: 18.8	2: 0.0	3: 0.0	2.688 ± 0.506	0: 25.0	1: 18.8	2: 37.5	3: 18.8
80	0.125 ± 0.085	0: 87.5	1: 12.5	2: 0.0	3: 0.0	3.563 ± 0.387	0: 6.3	1: 18.8	2: 37.5	3: 37.5

^a Cover expressed in codes, where 0 = *M. globulosella* not present, 1 = < 10 cm², 2 = 10 - 400 cm² and 3 = > 400 cm² cover on trees.

In general, a high percentage of the test subplots in young stands showed low cover values of 0 and 1 with few subplots showing higher cover values of 2 and 3 (Table 5).

Lichen cover increased significantly in young stands with stand age in both n = 19 (Table 6) and in n = 16 (Table 7).

Table 6. OLR analysis for *Micarea globulosella* cover for n = 19. Significant values are highlighted in bold. Coefficients indicate a negative or positive effect.

	Young stands; n = 19		Old stands; n = 19	
	Coefficient	P-value	Coefficient	P-value
Distance to stand edge (m)	-0.018	0.071	0.012	0.134
Stand age (years)	0.157	0.006	0.103	< 0.001
Stand elevation (m)	0.016	0.103	0.021	< 0.001
Water area (ha) within 300 m / 1000 m virtual buffer	2.783/ n.a. ^b	0.047 / n.a. ^b	2.782/ n.a. ^b	0.012 / n.a. ^b
Latitude (x-coordinate)	< -0.001	0.165	< 0.001	0.011
Longitude (y-coordinate)	< 0.001	0.919	0.001	< 0.001
Near calculation: stand edges to open water bodies	0.002	0.058	0.002	0.005
Near calculation: stand edges to wetlands within 1000 m radius	-0.003	0.257	-0.004	0.109
Area old forest within 100 m buffer centred in young forest stands	-0.141	0.674	0.160	0.393
Area old forest within 1000 m buffer centred in young forest stands	-0.004	0.765	0.016	0.146
Number of trees occupied by <i>M. globulosella</i> in old stands	n.a. ^c	n.a. ^c	n.a. ^b	n.a. ^b
^b Not tested				
^c Not tested due to error resulting from R "Design" Package				

Table 7. OLR analysis for *Micarea globulosella* cover for n = 16. Outlier stands number 20, 21 and 23 were omitted from this test. Significant values are highlighted in bold. Coefficients indicate a negative or positive effect. Note that Distance, among other co-variables, is significant in this OLR while it is not significant in the n = 19 OLR.

	Young stands; n = 16		Old stands; n = 16	
	Coefficient	P-value	Coefficient	P-value
Distance to stand edge (m)	-0.025	0.035	0.008	0.317
Stand age (years)	0.121	0.010	0.107	0.010
Stand elevation (m)	< 0.001	0.998	0.024	< 0.001
Water area (ha) within 300 m / 1000 m virtual buffer	0.811/ n.a. ^b	0.574/ n.a. ^b	2.593/ n.a. ^b	0.061/ n.a. ^b
Latitude (x-coordinate)	< 0.001	0.357	< 0.001	0.409
Longitude (y-coordinate)	< 0.001	0.738	< 0.001	< 0.001
Near calculation: stand edges to open water bodies	0.001	0.161	0.002	0.111
Near calculation: stand edges to wetlands within 1000 m radius	0.003	0.320	-0.005	0.137
Area old forest within 100 m buffer centred in young forest stands	-0.191	0.557	0.258	0.282
Area old forest within 1000 m buffer centred in young forest stands	n.a. ^b	n.a. ^b	0.012	0.439
Number of trees occupied by <i>M. globulosella</i> in old stands	n.a. ^c	n.a. ^c	n.a. ^b	n.a. ^b
^b Not tested				
^c Not tested due to error resulting from R "Design" Package				

***Micarea globulosella* occupancy and cover – old stands**

The mean number of trees occupied by *M. globulosella* in the old stands out of a maximum occupancy value of 5 was 3.074 ± 0.192 for n = 19 and 3.050 ± 0.214 for n = 16, respectively. The mean lichen cover out of a maximum cover value of 3 was 1.832 ± 0.112 for n = 19 and 1.813 ± 0.126 for n = 16 stands, respectively. There was a higher mean *M. globulosella* cover in old stands compared to the young stands (Wilcoxon rank sum test, $p < 0.001$; Figure 3).

For both n = 19 and n = 16, *M. globulosella* cover was relatively uniform in the old stands, with a more similar percent of trees showing cover values of 0 – 3 than in the young stands (Table 5). Cover values were higher in the old stands than in the young stands. A greater percentage of test subplots showed high cover values of 2 and 3 and a low percentage showed cover values of 0 and 1 (Table 5). Lichen occupancy increased significantly with stand age in old stands in both n = 19 (Table 3) and n =

16 (Table 4). Lichen cover increased significantly with stand age in old stands in both n = 19 (Table 6) and n = 16 (Table 7) stands.

***Micarea globulosella* edge effect study**

The following results are for both n = 19 and n = 16. When distance from edge was tested as a single variable (i.e. without co-variables) in a GLM, N and S-facing young stands showed a significant decrease in lichen occupancy with increasing distance from the forest edge towards the forest interior of the young stand (Table 8). An opposite effect was found in old S-facing stands, where there was a significant increase in *M. globulosella* occupancy with increasing distance from the stand edge into the forest interior (Table 8). With the variables used in this GLM model, no edge effects could be detected for old stands with N-facing edges. Figure 6 visually represents these results. Note that at all distances, 5 m, 20 m, 40 m, 60 m and 80 m from the stand edge, the occupancy is higher in the old than in the young stands, as can be seen by the trend line (Figure 6).

Table 8. Results of GLM analyses which tested *Micarea globulosella* occupancy with increasing distance from the stand edges. Table shows test results for young stands with N edge aspects, S edge aspects, for old stands with N edge aspects, S edge aspects, and for all young and all old stands, respectively. Values for n = 19 and n = 16 are shown. Significances and estimates remain similar, regardless of n = 19 or n = 16 and are shown in bold type. Estimates indicate a negative or positive effect.

	Young stands; n = 19		Old stands; n = 19		Young stands; n = 16		Old stands; n = 16	
	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value
N edge aspect	-1.643	< 0.001	-0.158	0.541	-2.032	< 0.001	-0.336	0.227
S edge aspect	-1.738	< 0.001	0.522	0.024	-1.562	0.001	0.671	0.010
All young	-1.682	< 0.001	n.a.	n.a.	-1.846	< 0.001	n.a.	n.a.
All old	n.a.	n.a.	0.231	0.175	n.a.	n.a.	0.219	0.236

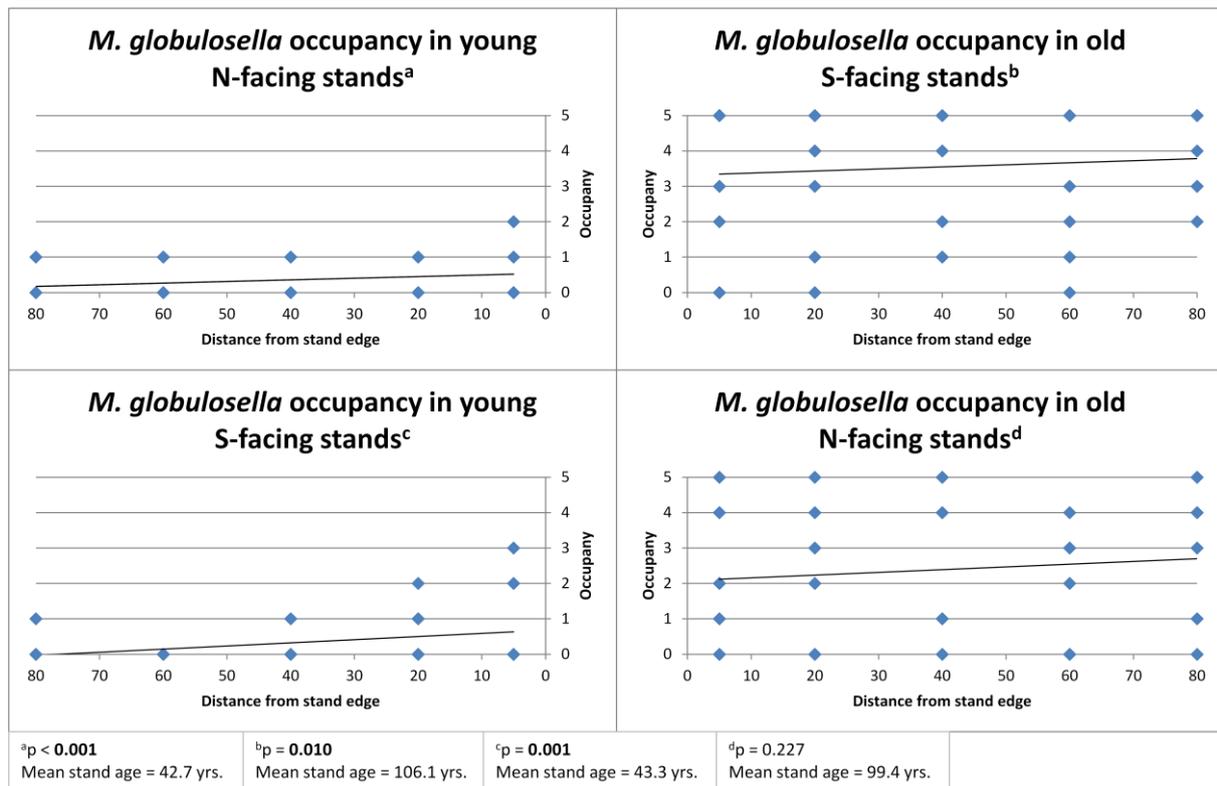


Figure 6. *M. globulosella* occupancy at 5 m, 20 m, 40 m, 60 m and 80 m from the stand edge into the forest interior for young N, old S, young S and old N-facing stands for n = 16. P-values and mean stand ages are given below the graphs.

In line with the results from Table 8, lichen cover decreases with distance to the stand edge in young stands of n = 16 when the variable is tested in an OLR model (Table 7).

Effects of the sum of occupied trees in adjoining old stands on *Micarea globulosella* occupancy in young stands

With an increase in the number of trees occupied by *Micarea globulosella* in the directly opposite old stands, there was a significant increase in lichen occupancy in the young stands in both n = 19 (Table 3) and in n = 16 (Table 4).

Effects of other co-variables on *Micarea globulosella* occupancy and cover in young and old stands

A significant negative effect of latitude on lichen occupancy was found in young stands for $n = 19$. On the contrary, a significant positive effect of latitude on occupancy was found in old stands for $n = 19$ (Table 3). This observation is further supported by a significant positive effect of latitude on lichen cover found in old stands for $n = 19$ (Table 6). A significant positive effect of open water on *Micarea globulosella* occupancy in old stands in $n = 19$ (Table 3), and in $n = 16$ (Table 4) was found. Also, a significant positive effect of water on cover in $n = 16$ was found in old stands (Table 6). Table 3 shows a significant positive effect on lichen occupancy in old stands of $n = 19$ when water is present within 300 m from the stand edge (H₂O 300). Lichen cover shows a significant positive effect of H₂O 300 in both old and young stands of $n = 19$ (Table 6). Similar to $n = 19$, Table 4 ($n = 16$) shows a significant positive effect of H₂O 300 on occupancy in old stands. Contrary to expectations, H₂O 300 has a negative effect on occupancy in young stands of $n = 16$. For $n = 16$ a significant positive effect of elevation on occupancy was found (Table 4). In support of this finding, a significant positive effect of elevation on cover was shown in old stands of $n = 19$ (Table 6) and in old stands of $n = 16$ (Table 7). Table 4 shows a significant positive effect of longitude on lichen occupancy in old stands for $n = 16$. Longitude also shows a significant positive effect on cover in old stands of $n = 19$ (Table 6) and of $n = 16$ (Table 7). A significant positive effect of Old Forest 1,000 on lichen occupancy was found in old stands for $n = 16$. Distance Wetlands shows a significant negative effect on lichen occupancy in young stands of $n = 19$ (Table 3). Finally, Distance Water shows a significant positive effect on lichen cover in old stands for $n = 19$ (Table 6).

Differences between n = 19 and n = 16

In general, there were some differences in significances in n = 16 that did not show up in n = 19. For example, the co-variable Distance was not significant in the n = 19 GLM, whereas the same co-variable was significant in the n = 16 GLM. However, significances that were found in GLMs and OLRs of n = 19 frequently appeared in n = 16 calculations. For example, the significant positive effect of stand age on cover in the n = 19 OLR is also observed in the n = 16 OLR.

Discussion

Main results of this study

This study reveals a variety of new ecological observations on the *Micarea globulosella* lichen species. Results show that the lichen can successfully grow and establish itself in young and regenerating *P. abies* stands, however with a lower occupancy and cover than in old forest stands. Secondly, results show that *M. globulosella* occupancy and cover is impacted by edge effects. More specifically, microclimate and dispersal are probably the two factors found at the stand edges that have the greatest impact on lichen occupancy and cover, according to results.

Occupancy in young stands

Previously, *Micarea globulosella* was thought to be an old-growth lichen species growing in forests with high humidity and long tree continuity (Thor & Arvidsson 1999). Results support the hypothesis

that *M. globulosella* has a higher occupancy and cover in old forest stands and lower occupancy and cover in young stands.

M. globulosella was found to have a mean occupancy and cover greater than 0 at all young stand test subplots. This finding may indicate two ecological implications for the lichen species. Firstly, the results suggest that the lichen may have an efficient dispersal mechanism since it occurs frequently on young *P. abies* trunks of 30 - 70 years old. It is known that *M. globulosella* spores are approximately $13\ \mu\text{m} - 26\ \mu\text{m} \times 1.5\ \mu\text{m} \times 3\ \mu\text{m}$ in size (Thor & Arvidsson 1999). Ascospores from the lichen mycobiont are ejected between 3 mm and 50 mm from the thallus and dispersed by wind and water. Wind speeds above $5\ \text{ms}^{-1}$ are necessary for spore dispersal, and with wind speeds around $30 - 35\ \text{ms}^{-1}$, spores can be transported over long distances (Seaward 2008). Hence, *M. globulosella* may have an effective enough dispersal mechanism to create an ample background propagule rain, similar to the observations Hylander (2009) made with boreal bryophytes. If the lichen would have a poor or short-distance dispersal capability, for example via symbiotic thallus fragments, a greater drop in lichen occupancy would be expected when moving further into the young stands and away from the old stands, as noted by Dettki et al. (2000) for the fruticose pendulous *Bryoria* spp. and the foliose *Hypogymnia* spp. lichens. Secondly, a possible parallel implication of this observation may be that the photobiont, i.e. green algae, necessary for lichen symbiosis is dispersed throughout the entire forest and when the *M. globulosella* ascomycete mycobiont spores come into contact with this alga, successful symbiosis can occur. Hedenås et al. (2007) suggest that the presence of free-living photobiont algae in *Populus tremula* retention stands may be the prerequisite for the re-establishment of spore-dispersed lichen species populations. As *M. globulosella* is a spore-dispersed lichen, this mechanism of encountering a free-living photobiont necessary for lichenisation, as indicated by Hedenås et al. (2007), may also occur in *M. globulosella*.

Another possible theory is that the mycobiont spores carry the photobiont algae together via wind, water and animal dispersal (Göran Thor, *personal communication*). Additionally, entire fragments of the lichen thallus may break off and be transported by wind, water and animals. Dettki et al. (2000) suggest that one of the mechanisms of *Bryoria* spp. reproduction occurs via the dispersal of thallus fragments. Reproduction via thallus fragments has never been observed in *M. globulosella*, but a dispersal via thallus fragments is a plausible suggestion for lichen reproduction and can be observed in a number of other lichen species, as discussed in this paper's literature review.

The theories presented above are speculative, since the exact dispersal mechanisms of *M. globulosella* are yet unknown. No further ecological studies have been conducted on *M. globulosella* dispersal, growth and lichenisation mechanisms which support the theories presented in this paper. Further research on *M. globulosella* and other crustose lichen species and their dispersal mechanisms is highly recommended, as dispersal of crustose lichen species is still a new and unstudied field.

Edge effects

Results from this study show that *Micarea globulosella* can grow on S-facing stand edges under less favourable microclimatic conditions, however lichen occupancy declines with proximity to the stand edge on S-facing edges in young as well as old stands. This could indicate that the crustose *M. globulosella* lichen may not be as sensitive to microclimatic and solar radiation variations as other lichen and bryophyte species, including *Alectoria sarmentosa* (Esseen & Renhorn 1998), *Usnea longissima* (Jansson et al. 2009), *Platismatica glauca* and *Lobaria pulmonaria* (Renhorn et al. 1997), and the bryophyte species *Hylocomium splendens* and *Hylocomiastrum umbratum* (Hylander 2005), which show a stronger response to stand edges and the associated less favourable growth and

microclimate, including increased light, wind conditions and greater temperature fluctuations and lower humidities. Results from this study may indicate that *M. globulosella*, similar to other crustose lichens, is less sensitive to abrupt environmental changes, as observed by Hilmo and Holien (2002) than pendulous or fruticose lichen species. Büdel & Scheidegger (2008) also discuss that crustose lichens are adapted to and thrive on bare substrates and under adverse (micro-) climatic conditions.

Results show that stand edges have an effect on *M. globulosella* occupancy in both young and old stands with N and S-facing edge aspects. Edge effects on S-facing aspects in young and old forests were expected due to a less favourable microclimate at S-facing stand edges, but contrary to expectations, an edge effect was also found in young stands with N-facing edges. At N-facing stand edges the highest occupancy was found closest to the directly adjacent old forest stands. Also, a decrease in occupancy closer to S-facing stand edges was expected for young stands, due to a less favourable microclimate with greater temperature fluctuations and lower relative humidity close to the stand edges. The observations show the contrary. *M. globulosella* occupancy decreases with distance from the stand edge. This could be explained by the following two theories. Firstly, Coxson & Stevenson (2007) noted an increase in *L. pulmonaria* growth near the forest edge, provided that the forest edge is “soft” and not “hard” or abrupt. In my case a “soft” edge is present. According to Coxson & Stevenson (2007) “hard” edges are found between old forests and clear-cuts, where large stand age or landscape differences occur. In my case, many of the young stands are medium-aged with trees between 40 and 70 years of age. These young stands border old stands with dominating tree layers of approximately 95 to 125 years of age. This age difference between young and old stands is not exceedingly large and thus many “soft” edges are present in my n = 19 and n = 16 stands. Coxson & Stevenson (2007) found that *L. pulmonaria* responds positively to increased light at “soft” edges with 30 - 40% canopy openness. At the same time, at “hard” edges with canopy openness exceeding 40%, *L. pulmonaria* growth decreases despite greater light exposure. A more

rapid drying of thalli as a result of greater exposure and higher levels of convection at the stand edges compensates for greater light exposure and thus *L. pulmonaria* growth is decreased (Coxson & Stevenson 2007). In my case, *M. globulosella* may have benefitted from greater light exposure of a “soft” edge, but may still have benefitted from less exposure due to an overall high stand age.

The second explanation for why *M. globulosella* showed the highest occupancy in young S-facing stands may be due to dispersal (via mycobiont spores or symbiotic thallus fragments) overriding microclimate effects at the forest edge. At young S-facing stand edges, there may be a dispersal effect from the directly opposite N-facing old stands, which show high lichen occupancy and cover. If *M. globulosella* dispersal should be effective and persistent (future studies have yet to show *M. globulosella* dispersal mechanisms), then dispersal from the N-facing old stand into the S-facing young stand may be strong enough to counteract and override the dry and harsh microclimatic fluctuations found directly at the stand edge.

Thirdly, as young S-facing stands are directly opposite of old N-facing stands, shading from the old N-facing stands may be a factor contributing to a more moderate microclimate directly at the edge of the young S-facing stands. With a moderate stand edge microclimate (minimal temperature and humidity fluctuations, less weathering) *M. globulosella* could successfully establish itself along the edge of the young S-facing stand. If this was the case, I would expect that there would be a gradient in occupancy. The highest *M. globulosella* occupancy would be expected closest to the adjacent N-facing old stand, at 5 m from the stand edge. This would be due to lichen dispersal via mycobiont spores or symbiotic thallus fragments dispersing from the old N-facing stand into the young S-facing stand.

The contrary is observed in old S-facing stands, where lichen occupancy increases with distance from the stand edge and towards the stand interior. This result could be attributed to the reduced edge effects further into the forest interior, as noted by Esseen & Renhorn (1998), and a more favourable microclimate with cooler temperatures, lower temperature fluctuations and moister air further away from the forest edge (Chen et al., 1995).

Results of this edge effect study are unexpected, especially for young S-facing stands, and perhaps with a pendulous lichen such as *A. sarmentosa* we may have observed a change in growth as other researchers have, such as in Esseen & Renhorn (1998). At the same time, it is impossible to make concrete statements on changes in microclimate at the forest edges in this study since meteorological measurements are lacking. For future studies, if time and funding permit, including empirical meteorological data for all 19 stands and at the test subplots would greatly enhance the observations of this and future studies. This way possible temperature, solar radiation and humidity fluctuations near the stand edges and into the young and old forest interior could be factored into the results.

Additionally, effects of nitrogen on *M. globulosella* growth at the stand edges cannot be discussed as it still remains unknown how this lichen species responds to increases in nitrogen exposure via deposition or fertilisation. Lichen nitrogen responses to fertilisation and deposition are highly species specific, with some lichens such as *Evernia prunastri* (L.) Ach. compromised by increases in nitrogen supplies (Munzi et al. 2010), while other lichen species such as *Xanthoria parietina* (L.) Th.Fr. show greater tolerance to increases in nitrogen loads. Further studies on *M. globulosella* responses to various nitrogen loads are recommended.

Differences between n = 19 and n = 16

There are a number of co-variables that have a significant effect on *Micarea globulosella* occupancy and cover in the n = 16 GLM and not in the n = 19 GLM. Examples are distance, elevation, longitude and area of old forest surrounding the young stands, which show significant effects in the n = 16 GLM but not in the n = 19 GLM. The same is true for the n = 16 OLR and the n = 19 OLR. Outlier stands number 20, 21 and 23 had unusually high occupancy and cover values compared to the other 16 stands and thus changed the outcomes of the statistical analyses. Possible factors that may have contributed to the unusual data of these stands include the following. Firstly, outlier stands 20, 21 and 23 were much further south than the other 16 stands. This may explain the significant positive effect of latitude in the n = 19 GLM and the n = 19 OLR tests for occupancy and cover. Secondly, the mean stand age was greatest in stands 20, 21 and 23, compared to the rest of the young stands.

If this paper were to be published in a scientific journal, I would choose to use results from the n = 16 tests due to the following reasons. The n = 16 samples are more homogeneous in occupancy, cover and in location, and recorded values in n = 16 are more representative of the values recorded in the rest of the young stands.

Other co-variables

A number of other co-variables had significant effects on *Micarea globulosella* occupancy. These include (i) a significant positive effect of a high lichen occupancy in old stands on the occupancy in young stands for n = 19 (Table 3) and n = 16 (Table 4), probably due to lichen dispersal of either spores or symbiotic lichen thallus fragments, (ii) a significant positive effect of Distance Water on

lichen occupancy in n = 19 (Table 3) and n = 16 (Table 4), probably due to a more favourable (cooler and moister) microclimate of the close proximity of water bodies on lichen growth, (iii) a significant negative effect of water within 300 m of the test subplots in young stands, and a significant positive effect on lichen occupancy in old stands of n = 16, and others (see Tables 3, 4, 6 and 7). I cannot make concrete explanations as to why some co-variables were significant, e.g. a significant negative effect and a significant positive effect of latitude on *M. globulosella* occupancy in young and old stands, respectively. A possibility is that type I errors (false positive) or a type II (false negative) errors may have occurred, and thus some calculations with co-variables may have resulted in significant positive or negative effects.

Recommendations for maintaining stable *Micarea globulosella* populations

This study has shown that *Micarea globulosella* can grow in young forest stands in boreal Sweden, but occupancy and cover is highest in older stands aged between 90 and 125 years of age. Currently Swedish forests are harvested between 90 – 100 years of age. In the future Swedish forests will be harvested at the younger age of about 70-80 years depending on climatic factors, including elevation, in order to maximise production. According to the results of this study, future younger stands may significantly diminish *M. globulosella* occupancy and cover. Still, according to this study's results, *M. globulosella* will continue to grow and disperse in younger forests, contrary to what was previously believed. Tree retention patches, including nature reserves and areas where old *P. abies* trees are maintained and protected, may serve as good reserves for higher *M. globulosella* cover and occupancy levels and possibly also a propagule source for lichen regeneration in younger intensive production stands.

The preservation of *M. globulosella* would be predominantly for the preservation of forest biodiversity. Other use of *M. globulosella* for example as an indicator species is not practical. One of the main prerequisites for indicator species is that they are easily detectable. As accurately recognising *M. globulosella* requires time, a magnifying glass or a microscope, and to be certain bioanalytical methods, this lichen species is not practical for use as an indicator species.

Strengths and weaknesses of this study

This study shows both strengths and weaknesses. A strength of this study is that both young and old stands were considered as a pair. As only few ecological studies exist where both young and old stands were tested together, this study is valuable and shows interactions between directly adjacent young and old forest stands. With already intense forest resources use and projected intensification of forest resources use in the future, forest landscapes are predicted to become more fragmented. With increases in forest fragmentation, greater areas of forest edge habitat are expected. This paper studies the ecological responses of a lichen in a fragmented forest, which is similar to a future fragmented forest landscape.

While this study is powerful, it lacks several points. First of all, no meteorological data was factored into the models. Meteorological data would allow for a more accurate statement on how strong the edge effect really is and how much the microclimate differs from the forest interior to the stand edges. Secondly, the trees in the old stands have a fairly young mean age of 104.8 years. Older trees would allow for better conclusions on what happens to *M. globulosella* on older trees. Currently there are still several questions unanswered. What happens to *M. globulosella* on older trees and

does the occupancy and cover continue to increase in a linear fashion on old trees? Does the *M. globulosella* occupancy and cover decrease beginning from a certain host age? Currently, data and models do not allow for explanations.

Finally, studying *M. globulosella* ecology and edge effects in stands which are individually considered and not paired may be interesting, however that experiment would study different research questions, than the ones posed in this study.

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Appendix

Appendix 1. Stand information from the 2002 *M. globulosella* survey and forest company Holmen Skog.

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in 5 subplots
1	young	33	5	0	0	N	350	0	1548508	1002.394	229.313	0
1	young	33	20	0	0	N	350	0	1548508	1002.394	229.313	0
1	young	33	40	0	0	N	350	0	1548508	1002.394	229.313	0
1	young	33	60	0	0	N	350	0	1548508	1002.394	229.313	0
1	young	33	80	0	0	N	350	0	1548508	1002.394	229.313	0
2	young	58	5	2	2	N	280	0	1542999	1552.729	198.375	5
2	young	58	20	1	1	N	280	0	1542985	1552.729	198.375	5
2	young	58	40	1	1	N	280	0	1542966	1552.729	198.375	5
2	young	58	60	1	1	N	280	0	1542952	1552.729	198.375	5
2	young	58	80	0	0	N	280	0	1542932	1552.729	198.375	5
3	young	33	5	2	1	S	310	0	1552999	2216.97	134.063	4
3	young	33	20	2	1	S	310	0	1553012	2216.97	134.063	4
3	young	33	40	0	0	S	310	0	1553030	2216.97	134.063	4
3	young	33	60	0	0	S	310	0	1553047	2216.97	134.063	4
3	young	33	80	0	0	S	310	0	1553063	2216.97	134.063	4
4	young	48	5	0	0	N	220	1.133	1549342	76.28	216.063	2
4	young	48	20	0	0	N	220	1.133	1549323	76.28	216.063	2
4	young	48	40	1	1	N	220	1.133	1549304	76.28	216.063	2
4	young	48	60	1	1	N	220	1.133	1549288	76.28	216.063	2
4	young	48	80	0	0	N	220	1.133	1549268	76.28	216.063	2
5	young	30	5	0	0	S	190	0	1558842	1353.942	186.625	1
5	young	30	20	1	1	S	190	0	1558842	1353.942	186.625	1
5	young	30	40	0	0	S	190	0	1558850	1353.942	186.625	1
5	young	30	60	0	0	S	190	0	1558863	1353.942	186.625	1
5	young	30	80	0	0	S	190	0	1558868	1353.942	186.625	1
6	young	59	5	0	0	S	280	0	1545552	662.431	216.688	1
6	young	59	20	0	0	S	280	0	1545565	662.431	216.688	1
6	young	59	40	1	1	S	280	0	1545580	662.431	216.688	1
6	young	59	60	0	0	S	280	0	1545604	662.431	216.688	1
6	young	59	80	0	0	S	280	0	1545604	662.431	216.688	1

(Continued)

Appendix 1. continued

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in each subplot
9	young	38	5	3	2	S	370	0	1546714	1532.933	165.688	4
9	young	38	20	1	1	S	370	0	1546704	1532.933	165.688	4
9	young	38	40	0	0	S	370	0	1546682	1532.933	165.688	4
9	young	38	60	0	0	S	370	0	1546661	1532.933	165.688	4
9	young	38	80	0	0	S	370	0	1546642	1532.933	165.688	4
10	young	40	5	0	0	S	160	1.161	1548601	223.019	155.125	0
10	young	40	20	0	0	S	160	1.161	1548613	223.019	155.125	0
10	young	40	40	0	0	S	160	1.161	1548629	223.019	155.125	0
10	young	40	60	0	0	S	160	1.161	1548645	223.019	155.125	0
10	young	40	80	0	0	S	160	1.161	1548662	223.019	155.125	0
11	young	70	5	0	0	S	240	0	1549312	461.979	240.5	1
11	young	70	20	0	0	S	240	0	1549311	461.979	240.5	1
11	young	70	40	0	0	S	240	0	1549308	461.979	240.5	1
11	young	70	60	0	0	S	240	0	1549305	461.979	240.5	1
11	young	70	80	1	1	S	240	0	1549300	461.979	240.5	1
12	young	70	5	0	0	N	200	0.119	1549454	265.477	258.313	4
12	young	70	20	1	1	N	200	0.119	1549469	265.477	258.313	4
12	young	70	40	1	1	N	200	0.119	1549488	265.477	258.313	4
12	young	70	60	1	1	N	200	0.119	1549508	265.477	258.313	4
12	young	70	80	1	1	N	200	0.119	1549526	265.477	258.313	4
13	young	30	5	0	0	N	120	1.079	1553705	69.056	109.188	0
13	young	30	20	0	0	N	120	1.079	1553690	69.056	109.188	0
13	young	30	40	0	0	N	120	1.079	1553669	69.056	109.188	0
13	young	30	60	0	0	N	120	1.079	1553648	69.056	109.188	0
13	young	30	80	0	0	N	120	1.079	1553628	69.056	109.188	0
14	young	35	5	0	0	N	370	0	1545349	1787.577	183.75	1
14	young	35	20	0	0	N	370	0	1545360	1787.577	183.75	1
14	young	35	40	1	1	N	370	0	1545378	1787.577	183.75	1
14	young	35	60	0	0	N	370	0	1545392	1787.577	183.75	1
14	young	35	80	0	0	N	370	0	1545409	1787.577	183.75	1
15	young	33	5	1	1	N	370	0	1540961	998.141	198.688	1
15	young	33	20	0	0	N	370	0	1540946	998.141	198.688	1
15	young	33	40	0	0	N	370	0	1540925	998.141	198.688	1
15	young	33	60	0	0	N	370	0	1540905	998.141	198.688	1

(Continued)

Appendix 1. continued

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in each subplot
15	young	33	80	0	0	N	370	0	1540885	998.141	198.688	1
16	young	38	5	2	1	N	360	0	1539681	1603.893	224.75	2
16	young	38	20	0	0	N	360	0	1539672	1603.893	224.75	2
16	young	38	40	0	0	N	360	0	1539661	1603.893	224.75	2
16	young	38	60	0	0	N	360	0	1539649	1603.893	224.75	2
16	young	38	80	0	0	N	360	0	1539639	1603.893	224.75	2
18	young	39	5	0	0	N	390	0	1524468	1054.323	195.438	1
18	young	39	20	1	1	N	390	0	1524457	1054.323	195.438	1
18	young	39	40	0	0	N	390	0	1524440	1054.323	195.438	1
18	young	39	60	0	0	N	390	0	1524425	1054.323	195.438	1
18	young	39	80	0	0	N	390	0	1524407	1054.323	195.438	1
19	young	33	5	0	0	S	310	0	1510221	745.226	196.375	0
19	young	33	20	0	0	S	310	0	1510236	745.226	196.375	0
19	young	33	40	0	0	S	310	0	1510256	745.226	196.375	0
19	young	33	60	0	0	S	310	0	1510278	745.226	196.375	0
19	young	33	80	0	0	S	310	0	1510298	745.226	196.375	0
20	young	40	5	0	0	N	240	0	1541970	1298.249	186	0
20	young	40	20	0	0	N	240	0	1541965	1298.249	186	0
20	young	40	40	0	0	N	240	0	1541958	1298.249	186	0
20	young	40	60	0	0	N	240	0	1541951	1298.249	186	0
20	young	40	80	0	0	N	240	0	1541943	1298.249	186	0
21	young	65	5	5	3	N	310	0	1544403	1503.126	231.063	21
21	young	65	20	4	2	N	310	0	1544400	1503.126	231.063	21
21	young	65	40	2	1	N	310	0	1544396	1503.126	231.063	21
21	young	65	60	5	2	N	310	0	1544391	1503.126	231.063	21
21	young	65	80	5	2	N	310	0	1544388	1503.126	231.063	21
23	young	49	5	1	1	S	340	0	1536234	1255.6	177.625	12
23	young	49	20	3	1	S	340	0	1536231	1255.6	177.625	12
23	young	49	40	1	1	S	340	0	1536225	1255.6	177.625	12
23	young	49	60	3	2	S	340	0	1536221	1255.6	177.625	12
23	young	49	80	4	2	S	340	0	1536215	1255.6	177.625	12
1	old	102	5	5	3	S	360	0	1548508	1002.394	229.313	24
1	old	102	20	5	3	S	360	0	1548519	1002.394	229.313	24
1	old	102	40	4	2	S	360	0	1548532	1002.394	229.313	24

(Continued)

Appendix 1. continued

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in each subplot
1	old	102	60	5	3	S	360	0	1548547	1002.394	229.313	24
1	old	102	80	5	3	S	360	0	1548561	1002.394	229.313	24
2	old	114	5	3	2	S	255	0	1543006	1552.729	198.375	22
2	old	114	20	4	2	S	255	0	1543019	1552.729	198.375	22
2	old	114	40	5	3	S	255	0	1543043	1552.729	198.375	22
2	old	114	60	5	2	S	255	0	1543062	1552.729	198.375	22
2	old	114	80	5	3	S	255	0	1543082	1552.729	198.375	22
3	old	96	5	4	3	N	330	0	1552990	2216.97	134.063	21
3	old	96	20	4	3	N	330	0	1552978	2216.97	134.063	21
3	old	96	40	4	3	N	330	0	1552960	2216.97	134.063	21
3	old	96	60	4	2	N	330	0	1552942	2216.97	134.063	21
3	old	96	80	5	3	N	330	0	1552928	2216.97	134.063	21
4	old	109	5	5	3	S	200	1.133	1549354	76.28	216.063	22
4	old	109	20	4	3	S	200	1.133	1549369	76.28	216.063	22
4	old	109	40	5	3	S	200	1.133	1549389	76.28	216.063	22
4	old	109	60	5	2	S	200	1.133	1549406	76.28	216.063	22
4	old	109	80	3	2	S	200	1.133	1549426	76.28	216.063	22
5	old	100	5	4	2	N	190	0	1558831	1353.942	186.625	19
5	old	100	20	3	1	N	190	0	1558829	1353.942	186.625	19
5	old	100	40	5	3	N	190	0	1558818	1353.942	186.625	19
5	old	100	60	2	1	N	190	0	1558809	1353.942	186.625	19
5	old	100	80	5	3	N	190	0	1558805	1353.942	186.625	19
6	old	95	5	0	0	N	280	0	1545541	662.431	216.688	10
6	old	95	20	0	0	N	280	0	1545522	662.431	216.688	10
6	old	95	40	4	3	N	280	0	1545502	662.431	216.688	10
6	old	95	60	3	2	N	280	0	1545480	662.431	216.688	10
6	old	95	80	3	1	N	280	0	1545461	662.431	216.688	10
9	old	96	5	5	3	N	380	0	1546723	1532.933	165.688	22
9	old	96	20	5	3	N	380	0	1546739	1532.933	165.688	22
9	old	96	40	5	3	N	380	0	1546756	1532.933	165.688	22
9	old	96	60	3	2	N	380	0	1546776	1532.933	165.688	22
9	old	96	80	4	3	N	380	0	1546794	1532.933	165.688	22
10	old	97	5	0	0	N	160	1.161	1548592	223.019	155.125	2
10	old	97	20	0	0	N	160	1.161	1548582	223.019	155.125	2

(Continued)

Appendix 1. continued

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in each subplot
10	old	97	40	1	2	N	160	1.161	1548565	223.019	155.125	2
10	old	97	60	0	0	N	160	1.161	1548546	223.019	155.125	2
10	old	97	80	1	1	N	160	1.161	1548534	223.019	155.125	2
11	old	104	5	2	1	N	240	0	1549311	461.979	240.5	9
11	old	104	20	2	1	N	240	0	1549312	461.979	240.5	9
11	old	104	40	1	1	N	240	0	1549314	461.979	240.5	9
11	old	104	60	0	0	N	240	0	1549317	461.979	240.5	9
11	old	104	80	4	2	N	240	0	1549320	461.979	240.5	9
12	old	96	5	2	1	S	190	0.119	1549442	265.477	258.313	7
12	old	96	20	1	1	S	190	0.119	1549430	265.477	258.313	7
12	old	96	40	1	1	S	190	0.119	1549408	265.477	258.313	7
12	old	96	60	0	0	S	190	0.119	1549391	265.477	258.313	7
12	old	96	80	3	2	S	190	0.119	1549370	265.477	258.313	7
13	old	115	5	0	0	S	120	1.079	1553717	69.056	109.188	5
13	old	115	20	0	0	S	120	1.079	1553732	69.056	109.188	5
13	old	115	40	2	1	S	120	1.079	1553749	69.056	109.188	5
13	old	115	60	1	1	S	120	1.079	1553769	69.056	109.188	5
13	old	115	80	2	1	S	120	1.079	1553789	69.056	109.188	5
14	old	96	5	5	3	S	370	0	1545340	1787.577	183.75	25
14	old	96	20	5	3	S	370	0	1545329	1787.577	183.75	25
14	old	96	40	5	3	S	370	0	1545311	1787.577	183.75	25
14	old	96	60	5	3	S	370	0	1545295	1787.577	183.75	25
14	old	96	80	5	2	S	370	0	1545280	1787.577	183.75	25
15	old	96	5	0	0	S	380	0	1540971	998.141	198.688	10
15	old	96	20	3	1	S	380	0	1540986	998.141	198.688	10
15	old	96	40	1	1	S	380	0	1541006	998.141	198.688	10
15	old	96	60	2	1	S	380	0	1541026	998.141	198.688	10
15	old	96	80	4	2	S	380	0	1541045	998.141	198.688	10
16	old	108	5	5	2	S	360	0	1539687	1603.893	224.75	24
16	old	108	20	4	2	S	360	0	1539696	1603.893	224.75	24
16	old	108	40	5	3	S	360	0	1539708	1603.893	224.75	24
16	old	108	60	5	3	S	360	0	1539719	1603.893	224.75	24
16	old	108	80	5	3	S	360	0	1539730	1603.893	224.75	24
18	old	119	5	5	3	S	350	0	1524478	1054.323	195.438	21

(Continued)

Appendix 1. continued

Stand Number ^a	Age	Stand Age (yrs.)	Distance from stand edge (m)	Occupancy (0 - 5) ^b	Cover (0 - 3) ^c	Stand Edge Aspect	Stand Elevation (m)	Open water within 300 m buffer (ha)	Longitude (y - coordinate)	Distance to open water bodies (m)	Area Old Forest 1000m Buffer (ha) ^d	Sum of trees occupied by <i>M. globulosella</i> in each subplot
18	old	119	20	5	3	S	350	0	1524491	1054.323	195.438	21
18	old	119	40	5	3	S	350	0	1524506	1054.323	195.438	21
18	old	119	60	3	2	S	350	0	1524525	1054.323	195.438	21
18	old	119	80	3	2	S	350	0	1524544	1054.323	195.438	21
19	old	108	5	1	1	N	320	0	1510212	745.226	196.375	1
19	old	108	20	0	0	N	320	0	1510195	745.226	196.375	1
19	old	108	40	0	0	N	320	0	1510175	745.226	196.375	1
19	old	108	60	0	0	N	320	0	1510155	745.226	196.375	1
19	old	108	80	0	0	N	320	0	1510135	745.226	196.375	1
20	old	100	5	0	0	S	270	0	1541974	1298.249	186	9
20	old	100	20	5	2	S	270	0	1541979	1298.249	186	9
20	old	100	40	1	1	S	270	0	1541986	1298.249	186	9
20	old	100	60	1	1	S	270	0	1541993	1298.249	186	9
20	old	100	80	2	1	S	270	0	1541000	1298.249	186	9
21	old	115	5	4	3	S	350	0	1544405	1503.126	231.063	20
21	old	115	20	2	2	S	350	0	1544409	1503.126	231.063	20
21	old	115	40	4	2	S	350	0	1544412	1503.126	231.063	20
21	old	115	60	5	3	S	350	0	1544417	1503.126	231.063	20
21	old	115	80	5	3	S	350	0	1544421	1503.126	231.063	20
23	old	125	5	3	2	N	330	0	1536236	1255.6	177.625	19
23	old	125	20	5	2	N	330	0	1536240	1255.6	177.625	19
23	old	125	40	4	2	N	330	0	1536245	1255.6	177.625	19
23	old	125	60	3	2	N	330	0	1536250	1255.6	177.625	19
23	old	125	80	4	3	N	330	0	1536254	1255.6	177.625	19

^aStand numbers of the three outliers which were omitted in the n = 16 calculations: 20, 21 and 23.

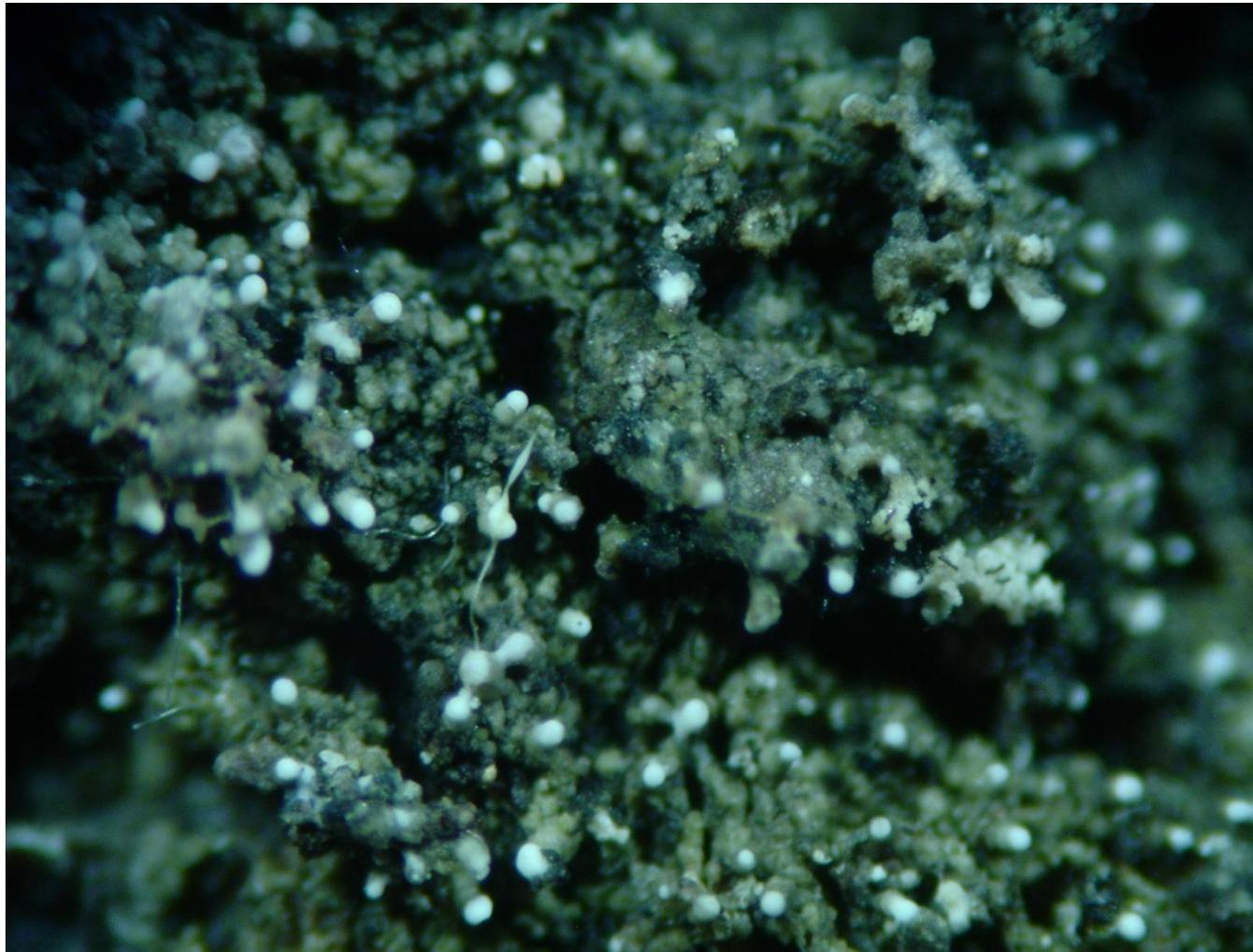
^bOccupancy data ranges from 0 of 5 trees occupied to 5 of 5 occupied in the test subplots.

^cCover expressed in codes, where 0 = *M. globulosella* not present, 1 = < 10 cm², 2 = 10 - 400 cm² and 3 = > 400 cm² cover on trees.

^dVirtual buffer centered in young stands and measured area of old forest surrounding the young stand.

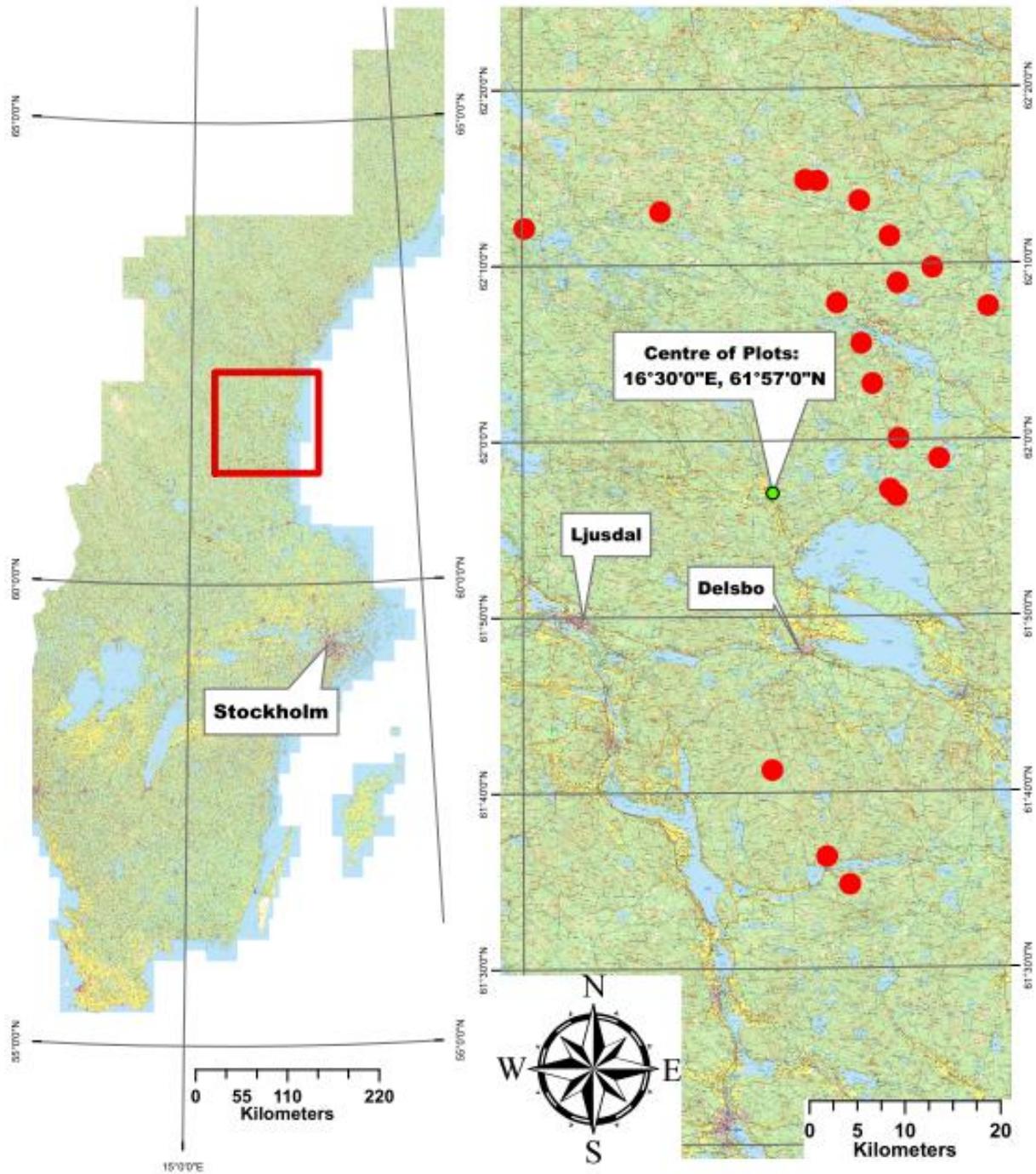


Appendix 2. This image shows *M. globulosella* on *P. Abies* bark. Sample was collected by Janolof Hermansson in Hälsingland during week 19 of 2002. Sample site was located 18.5 Km NW of Ramsjö. Lat/long: 62°17'N 15°32'E. Sample site altitude: 395 m. White globular *M. globulosella* pycnidia can be seen on bark.



Appendix 3. This image is a close-up of *M. globulosella* on *Betula* spp. bark. Sample was collected by Anders Nordin in Hälsingland during week 9 of 1993. Sample site was located 5.5 Km NE of Rullbo. Lat/long: 61°48'N 14°48'E. Sample site altitude: 430 m. This image shows greyish-green *M. globulosella* thalli with spherical pycnidia.

Overview of test subplots

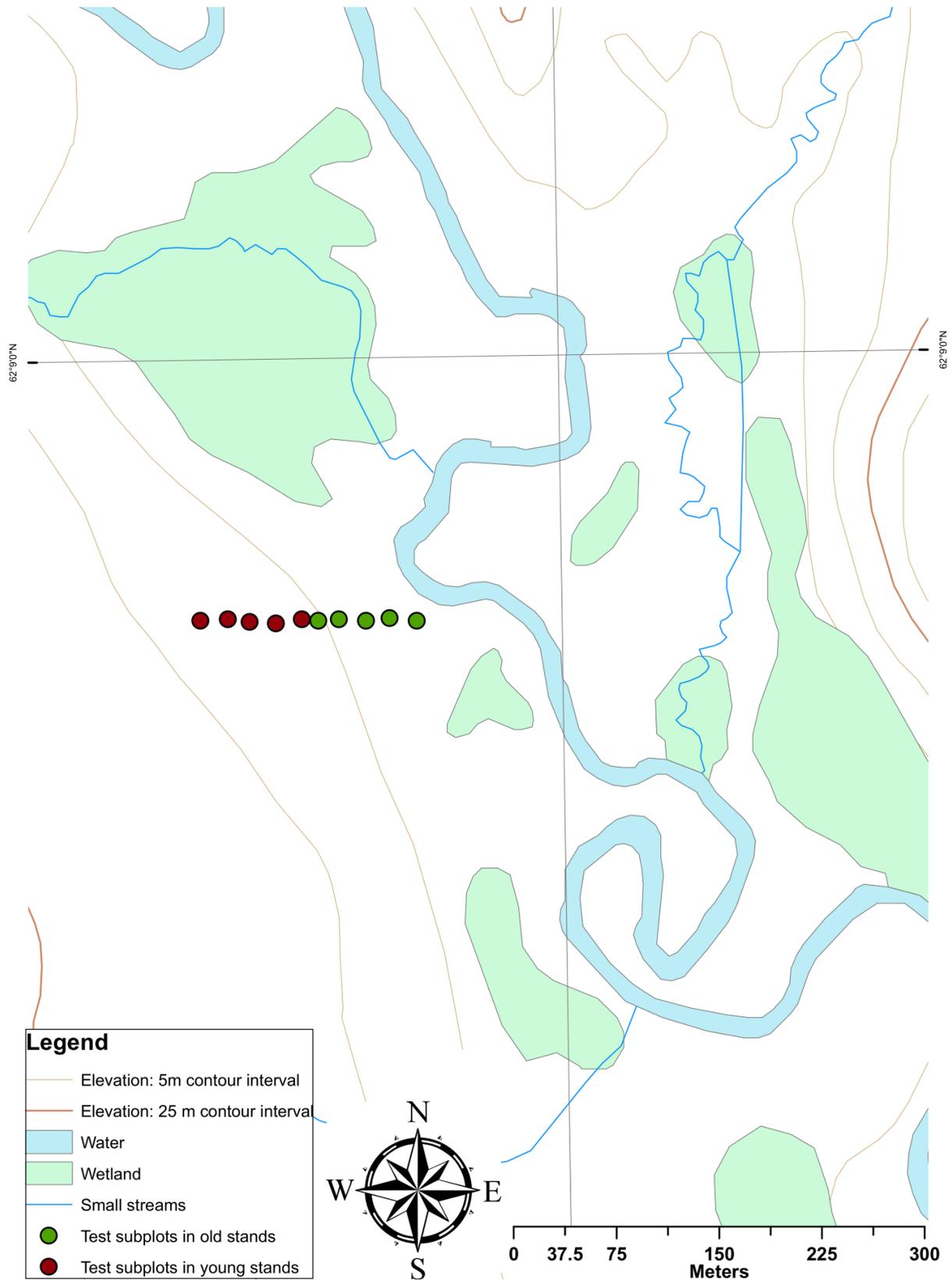


Legend

- *Micarea globulosella* test subplots

Appendix 4. Overview map of the *Micarea globulosella* test subplots. Test sites are located in boreal Sweden.

Sample of old and young test subplots



Appendix 5. Sample of old and young test plots. Stand edge aspect was visually evaluated.