

MASTER'S THESIS

Course code: BIO5010

Name: Linn Nefertari Leh

Spatial Population Dynamics of the Gravestone Lichen *Xanthoparmelia loxodes*

Date: 16.05.2022

Total number of pages: 31

Spatial Population Dynamics of the Gravestone Lichen

Xanthoparmelia loxodes

Romlig populasjonsdynamikk hos gravsteinlaven *Xanthoparmelia loxodes*



Figure 1 *Xanthoparmelia loxodes*, the brown lichen, on a gravestone (own photo).

Linn Nefertari Leh
tarileh@gmail.com

Supervisors:

Håkon Holien
hakon.holien@nord.no

Nord University

Kristian Hassel
kristian.hassel@ntnu.no
Norwegian University of
Science and Technology &
Nord University

Master in Biosciences: Terrestrial Ecology and Nature Management
Faculty of Biosciences and Aquaculture, Nord University

Steinkjer, 16.05.2022



Abstract

Background: Connectivity is a measure in the field of metapopulation dynamics that has become increasingly important with the amount of habitat loss and fragmentation in this age of urban expansion. The viability of populations in fragmented areas is measured through connectivity, with increased isolation and decreased size, the recolonization stays low, and extinction is high. Churchyards and cemeteries are a hotspot for urban biodiversity, especially for threatened species. To conserve biodiversity, this habitat should be looked at from a metapopulation perspective.

Aims: The aims are to 1) map the distribution of *X. loxodes* as presence/absence on the gravestones at Mære churchyard, 2) investigate if there is a significant difference between the proportion of rough and smooth textured stones through time, 3) calculate the colonization probability of *X. loxodes* on gravestones, and 4) test if the abundance of *X. loxodes* on the occupied stones is explained by a) connectivity or b) the substrate.

Method: During a survey of the 985 vertical gravestones at Mære churchyard, in the middle of Norway, the year of the first and last inscription of a gravestone was recorded. Additionally, the surface texture and surface area of the gravestone, *X. loxodes* occurrence, the diameter of the largest thallus, average size, number of thalli, competition status, and coverage of the stone were registered. Distance to the nearest occupied stone was calculated in ArcGIS Pro. A negative binomial generalized linear model and logistic regression were used to evaluate the effect of the explanatory variables on abundance and occurrence.

Results: *Xanthoparmelia loxodes* was found on 97 of the 985 surveyed gravestones. There was a significant difference between the proportion of rough and smooth textured gravestones through time. The colonization probability was affected by distance to the nearest occupied patch, age of the gravestone, and surface texture of the gravestone. The abundance was also affected by the distance, but the effect of gravestone age and surface texture were questionable. They both had an effect, but the extent is uncertain, due to conflicting results in different models.

Conclusion: Connectivity together with gravestone characteristics decides much of the distribution of *X. loxodes* at Mære. To conserve the biodiversity of churchyards and cemeteries, species should be evaluated from a metapopulation perspective.

Keywords: Metapopulation, churchyard, lichens, urban biodiversity, spatial distribution

Sammendrag

Bakgrunn: Konnektivitet er et mål innen metapopulasjonsdynamikk som har blitt stadig viktigere med det økende tapet av habitat og fragmentering i denne tiden av urban ekspansjon. Levedyktigheten til populasjoner i de fragmenterte områdene måles gjennom konnektiviteten mellom dem, med økt isolasjon og redusert størrelse, er rekoloniseringen lav, og utryddelsen høy. Kirkegårder og gravplasser er en hotspot for urbant biologisk mangfold, spesielt for truede arter. For å bevare det biologiske mangfoldet bør dette habitatet ses på med et metapopulasjonsperspektiv.

Målsetninger: Målene er å 1) kartlegge fordelingen av *X. loxodes* som til stede/fraværende på gravsteinene på Mære kirkegård, 2) undersøke om det er en signifikant forskjell mellom proporsjonen av ujevne og glatte gravsteiner gjennom tidene, 3) beregne koloniserings sannsynligheten for *X. loxodes* på gravsteiner, og 4) teste om mengden av *X. loxodes* på de okkuperte steinene er forklart av a) konnektiviteten eller b) substratet.

Metode: Ved en undersøkelse av de 985 vertikale gravsteinene på Mære kirkegård, i midten av Norge, ble året til den første og siste inskripsjonen av gravsteinen registrert. Overflateteksturen og overflatearealet på steinen, tilstedeværelse av *X. loxodes*, diameteren på det største thalluset, gjennomsnittlig størrelse, antall thalli, konkurransestatus og dekningsgrad på steinen ble også registrert. Avstand til nærmeste okkuperte stein ble beregnet i ArcGIS Pro. En negativ binomial generell liniær modell og logistisk regresjon ble brukt for å evaluere effekten av responsvariablene på tallrikheten og forekomsten.

Resultat: *Xanthoparmelia loxodes* ble funnet på 97 av de 985 undersøkte gravsteinene. Det var en betydelig forskjell mellom antall grovt og glatt teksturerte gravsteiner gjennom tidene. Koloniserings sannsynligheten ble hovedsakelig påvirket av avstand til nærmeste okkuperte stein, alder og overflatetekstur på gravsteinen. Tallrikheten ble også påvirket av avstanden, men effekten av alder på gravstein og overflatetekstur var tvilsom. De hadde begge en effekt, men omfanget er usikkert, på grunn av motstridene resultater i ulike modeller.

Konklusjon: Konnektiviteten sammen med gravstein karakterene bestemte mye av fordelingen av *X. loxodes* på Mære. For å bevare det biologiske mangfoldet på kirkegårder og gravplasser, bør arter vurderes fra et metapopulasjonsperspektiv.

Nøkkelord: Metapopulasjon, kirkegård, laver, urban biodiversitet, romlig fordeling

Acknowledgements

This is a master thesis with 60 credits in the graduate program *Biosciences with a Specialization in Terrestrial Ecology and Nature Management* at Nord University, Steinkjer, Norway.

I am grateful to my father Friedemann Leh for awakening my curiosity for lichens with his numerous long stops on our hiking and skiing trips just to take a few pictures of something I have never given much thought to, lichens. This curiosity grew into an interest during my bachelor's degree in Nature Management at Nord University in Steinkjer. Thank you to my two supervisors Håkon Holien and Kristian Hassel for helping with the study design and giving great feedback. I also want to thank Michael Patton for helping with the statistical analysis and results. Additionally, answering all my numerous questions. Without him, I would still be sitting here today trying to figure out the statistical analysis. A great thank you to my family members, especially my parents and my sister, for reading through my text several times and their feedback.

In addition, I need to thank my fellow lichen enthusiast Ingunn Hovland, for great company, being a sounding board, and much laughter during the fieldwork season at Mære churchyard. Lastly, I also need to give a great thank you to my roommate Katinka Svatun Eines for all her encouragement when I needed it.

Linn Nefertari Leh

Nord University

Steinkjer, May 2022

Table of Contents

| | |
|--|----|
| 1.0 Introduction | 1 |
| 1.1 Aims | 4 |
| 2.0 Materials and Methods | 4 |
| 2.1 Study species: <i>Xanthoparmelia loxodes</i> | 4 |
| 2.2 Study area | 5 |
| 2.3 Methods | 6 |
| 2.3.1 Orthophoto of the churchyard | 6 |
| 2.3.2 Data collection | 6 |
| 2.4 Connectivity measures | 7 |
| 2.5 Statistical analysis | 8 |
| 2.5.1 Gravestone fashion | 8 |
| 2.5.2 Colonization probability | 8 |
| 2.5.3 Assessment of species abundance | 9 |
| 3.0 Results | 9 |
| 3.1 Gravestone fashion | 11 |
| 3.2 Colonization probability | 11 |
| 3.3 Abundance of <i>X. loxodes</i> | 13 |
| 4.0 Discussion | 16 |
| 4.1 Connectivity | 16 |
| 4.2 Gravestone characteristics | 17 |
| 4.3 Gravestone fashion | 19 |
| 5.0 Conclusion | 19 |
| References | 1 |

1.0 Introduction

Habitat loss has become an increasing problem for the viability of species in this era of urban expansion (Hanski, 1998). Following extensive habitat loss, many species experience population decline and will consequently be rated as threatened and get red-listed if they fulfill certain criteria (Mace et al., 2008). Pure habitat loss is the main concern, with fragmentation, patch isolation, and patch size becoming an increasing problem the larger the habitat loss is (Andren, 1994; Hanski, 1998). Studies on how habitat loss and fragmentation affect the dynamics and fluctuations of populations through time and space on different scales have therefore become important. The introduction of the metapopulation concept (Levins, 1969) and the theory of island biogeography (MacArthur & Wilson, 1967) laid the foundation for the current research of metapopulation dynamics, where spatially separated populations that interact are studied (Hanski, 1998).

Today, the metapopulation concept incorporates colonization, extinction, patch size, patch isolation, migration, and dispersal to accurately predict population dynamics in a fragmented landscape (Hanski, 1999). The connectivity measure, in metapopulation ecology, is a patch-specific attribute (Moilanen & Hanski, 2001; Tischendorf & Fahrig, 2001) used to evaluate the isolation of subpopulations. The smaller and more isolated an area with a subpopulation in a metapopulation is, due to fragmentation and habitat loss, the higher the chance of extinction. Because of the isolated and small nature of the habitat, the chance of recolonization is low (Hanski, 1998). Therefore, it is important to either create linkages or preserve the remaining linkages between the habitat patches to minimize the extinction probability. Connectivity, the inverse of patch isolation or isolation by distance, has thus become an important aspect of biodiversity conservation (Crooks & Sanjayan, 2006). Connectivity, patch isolation, and isolation by distance measure the spatial configuration of habitat patches together with the occurrence of the study species and are therefore used interchangeably by researchers.

Connectivity is a measure that explains part of the spatial distribution of many populations in the wild by affecting, e.g., colonization rate (e.g. Biedermann, 2005; Hanski et al., 1994; Prugh et al., 2008), but it could also be a factor explaining the spatial distribution of species in urban areas found in, e.g., churchyards and cemeteries. Despite the orderly and kempt look of churchyards and cemeteries, they have some habitat heterogeneity with gravestones, walls, trees, buildings, roads, paths, and water features (Gilbert, 1991). The wide variety of rock types used as gravestones, e.g., sandstones, granites, gneisses, migmatites, slates, limestones, and

marbles contributes to this habitat heterogeneity (Morgan, 2016). Among the elements found in burial places, trees and gravestones, the two dominant substrates, are the most important. Through their age and various degrees of weathering and disintegration, they create several microhabitats for various species (Halda et al., 2020).

The habitat heterogeneity, size, and habitat stability of burial grounds create a possible hotspot for urban biodiversity (Buchholz et al., 2016). The high plant species diversity found in many churchyards and cemeteries (Halda et al., 2020; Kowarik et al., 2016; McBarron et al., 1988; Yilmaz et al., 2018) is caused by a possible remnant of native plants, the ornamental plants introduced by family members to decorate gravestones (Yilmaz et al., 2018), or the uniqueness of the area that causes rare plants to be preserved (Kowarik et al., 2016).

A species group that is positively influenced by churchyards and cemeteries as a habitat are lichens, especially saxicolous lichens. Burial places are one of the few areas in urban regions with suitable substrates, i.e., gravestones, for colonization by rock-inhabiting lichens (Halda et al., 2020). In Great Britain, over 630 lichen species have been recorded on or near trees in churchyards and cemeteries, gravestones, churches, abbeys, and cathedrals (Purvis, 2010). A few of the species have only been found in churchyards (Dennis, 1993).

Sessile species, e.g., lichens, are confined to their specific habitat. Their distribution will therefore be decided by their colonization ability, i.e., the dispersal and establishment of their propagules in different habitats. They are dispersed through either wind, water, or animals (Purvis, 2010). The morphological trait propagule mass in vascular plants, is a significant factor in the dispersal distance of active dispersers, but not for passive dispersers (Jenkins et al., 2007). No lichens were included in the study of Jenkins et al. (2007), but Leger and Forister (2009) later showed that propagule size was not a determining factor for the colonization ability of gravestone lichens. However, Norros et al. (2014) showed the opposite. They state that the dispersal is more complex for the smaller 1-10 μm spores of fungi and dependent on spore size. It is therefore not certain if the smaller sexually reproduced lichen spores disperse farther than the larger vegetatively produced ones. The larger spores were also more dependent on environmental conditions (Norros et al., 2014). The colonization ability may therefore also be affected by aspects like species' habitat requirements. For instance, the degree of deterioration of stones has an impact on the diversity of lichens (Owczarek-Kościelniak et al., 2020). The rough surface texture of stones provides also better anchoring points for biological colonization, compared to polished stones. Once colonized other factors like humidity are decisive for the

biological establishment of diaspores in general (Miller et al., 2012). These aspects are important to consider, as habitats like churchyards may be stable, but the species still must be able to track their preferred substrate (Snäll et al., 2005). In all, the mentioned factors are some of the factors that could affect the connectivity of sessile species.

Various measures can be used to calculate the connectivity between patches. The use of the distance metric distance to the nearest occupied patch, which explains much of the species distribution, is recommended by Prugh (2009). Other distance metrics used, are distance to all occupied patches (Hanski, 1999) and distance to the nearest habitat patch. In addition to the distance metrics, in accord with the metapopulation theory, patch size is included (Prugh, 2009). Patch size and patch isolation may not explain the whole picture regarding the species distribution. Habitat quality and quantity have also been shown to have a significant impact (e.g. Johansson et al., 2012; Ranius et al., 2008; Snäll et al., 2004). Tree size, tree quantity, tree species (Johansson & Ehrlén, 2003) and bark structure (Öckinger et al., 2005) are a few variables that have been used as habitat characteristics. It is also important to consider the dynamics of the substrate, e.g., trees, in addition to the population dynamics (Snäll et al., 2005). Although metapopulation aspects, e.g., distance and size, explain much of the distribution, the species still must be able to establish itself in its preferred habitat. Habitat characteristics should therefore be considered while studying distribution patterns.

Little research has been done regarding connectivity in churchyards and cemeteries. It has however been shown that lichen species on gravestones can be isolated by distance in urban habitats like churchyards and cemeteries, e.g., *Candelariella vitellina* (Warren, 2003). However, in this study isolation by distance was only shown in one of three cemeteries and for just one of two species, suggesting that more research is needed to investigate which factors influence the connectivity in churchyards and cemeteries. Furthermore, research is needed to assess how much isolation by distance affects the species distribution pattern, and if there are other factors influencing the distribution.

Looking beyond the possible connectivity in churchyards and cemeteries, the area of single churchyards and cemeteries and the biodiversity found there may be too small to contribute significantly to urban biodiversity. Yet when they are compiled together, they make up a considerable amount of area worthy of conservation consideration (Barrett & Barrett, 2001; Kendal et al., 2017). Old cemeteries and churchyards are especially of note in that regard (Yilmaz et al., 2018). These small urban habitats may furthermore contribute to the persistence

of dispersal-limited species by acting as stepping stones in the urban landscape (Dearborn & Kark, 2010). It is therefore important to consider churchyards and cemeteries as habitats with a considerable contribution to urban biodiversity.

1.1 Aims

Churchyards and cemeteries are places protected from urban expansion, thereby allowing for the original local flora or species not found anywhere else to persist. The motivation behind this project is to investigate the importance of burial places for urban biodiversity. Warren (2003) states that newly erected gravestones are a suitable system to study metapopulation dynamics since they represent habitat patches that are vacant, dated, and gradually duplicated in time. The present study uses a metapopulation perspective to map and understand the spatial pattern of the lichen species *Xanthoparmelia loxodes* at Mære church. The study is based on snapshot data, with a special focus on connectivity, growth, and dispersal.

The aim of this study is to 1) map the distribution of *X. loxodes* as presence/absence on the gravestones at Mære churchyard, 2) investigate if there is a significant difference between the proportion of rough and smooth textured stones through time, 3) assess the colonization probability of *X. loxodes* on gravestones, and 4) test if the abundance of *X. loxodes* on the occupied stones is explained by a) connectivity or b) the quality of the substrate (surface texture, age of gravestone, surface area).

2.0 Materials and Methods

2.1 Study species: Xanthoparmelia loxodes

The lichen genus *Xanthoparmelia* is one of the most diverse macrolichen genera and is estimated to contain over 800 species worldwide (Wirth, 2013). *Xanthoparmelia loxodes* is a foliose lichen that grows on rock surfaces (Figure 2), where siliceous rocks (e.g., granite), located on nitrogen-rich sites are preferred. The color of the thallus is dark brown to red-brown. It has a few black rhizines on the lower cortex, and it forms clusters of cauliflower-like isidia which eventually burst up in the tip where the white medulla becomes visible. Isidia is the main dispersal unit (Stenroos et al., 2021) and is sparsely to densely distributed on the surface (Smith et al., 2009). Apothecia are uncommon in this species and conidiomata are suspected to be rare according to Stenroos et al. (2021). The ascospores are ellipsoid and 8-10 x 4-5 μm , while the

size of the conidia is not known. *Xanthoparmelia loxodes* may be confused with *X. verruculifera*, which is also known from Norway, but that species is thinner with scattered, coarse isidia and contains different secondary metabolites (Smith et al., 2009).



Figure 2 2a) Left: A *Xanthoparmelia loxodes* thallus on a gravestone at Mære church (own photo), 2b) right: the known distribution of *X. loxodes* in Norway. The study area is located at the most northern red point on the map (Artdatabanken, n.d.; Kartgrunnlag: Kartverket (Creative Commons Attribution ShareAlike 3.0))

2.2 Study area

Mære churchyard was chosen as the study area, due to the population of *X. loxodes* being isolated there, as the northernmost location in Norway (Figure 2). Thus, it was assumed that there would be negligible background dispersal.

Mære church (63.93395184°N 11.394937187°E) is situated in Steinkjer municipality, Trøndelag county, in the middle of Norway. The church is located on a hill surrounded by agricultural fields near the Beitstad fjord in the southern boreal zone. The area is characterized by a slightly oceanic climate (Moen, 1998) with an average monthly temperature of -2.0 °C in January and 15.1 °C in July. The annual rainfall is around 827 mm (Klimaservicesenter, 2021) and the duration of the snow cover is around 3-5 months (Moen, 1998).

Mære church was built during the last part of the 11th century. The church has been restored and modified several times over the centuries. There were two main restoration projects, one in the 1650s and another in the 1960s. The purpose of the area as a church and a connected churchyard has remained the same (Nordberg & Mære, 1989). At Mære churchyard, the gravestones consist of primarily larvikite, gneiss, or granite, which are all acidic rock types (Schumann et al., 2000).

2.3 Methods

2.3.1 Orthophoto of the churchyard

The drone overview picture was taken on the 29th of April 2021, with a DJI Mavic 2 drone (Figure 4). The drone flew over a predetermined area, bounded by Google Earth. The drone pictures were merged with the program Agisoft Metashape (version 1.8.3).

2.3.2 Data collection

Data collection took place in the period August to October 2021. During the period, every vertical gravestone was surveyed (Figure 3). The variables recorded were the year of death of the first and last inscription. The surface area (cm²; based on width, length, and height) of the gravestone and the texture of the stone surface (rough, smooth) were also noted. When a *Xanthoparmelia loxodes* individual was found on a gravestone, the size of the largest thallus, the number of individual thalli, average size, competition status (winning, losing, winning and losing, no competition), and coverage (%) were evaluated and recorded. Coverage was evaluated by dividing the gravestone into eight sections with each consisting of 12.5% and afterwards visually estimating the amount of coverage. With each recording, the gravestone's running number was written on a printed drone overview picture, which was later imported into the program ArcGIS Pro version 2.8.6. A point with the gravestone's running number from the printed drone overview picture was created and placed above each gravestone in the orthophoto in ArcGIS Pro. The tool Near was used to calculate the distance to the nearest occupied gravestone. The wall around the churchyard was also investigated for *X. loxodes* thalli. If any were found, the size and location were recorded.



Figure 3 An example of a gravestone occupied mostly by the brown lichen *X. loxodes* (own photo).

2.4 Connectivity measures

The three most common methods to measure connectivity are buffer, nearest neighbor (NN), and the incidence function model (IFM; Prugh, 2009). Moilanen and Nieminen (2002) and Prugh (2009) both reviewed these measures. The connectivity models focus on different aspects of connectivity. Nearest neighbor is a distance-based measure, while buffer is an area-based measure. Each has its inherent weaknesses. The distance-based model NN does not consider the area around the patches and buffer not the distance to the nearest patch. The model IFM tries to correct for that by including both distance and buffer. It is a model that includes more information and is, therefore, more complex. Nearest neighbor is a common method to measure connectivity due to its minimal need for data. There is some discourse around which method is the most appropriate one and gives the most accurate outcome. IFM is widely recognized as a predictor that scores high. Nearest neighbor and buffer give varying results regarding predictor ability. According to Moilanen and Nieminen (2002), NN measures are too simplistic and give misleading results. Prugh (2009) however, showed the opposite. A variant of the NN model, the model nearest source (NSi), was shown to have a prediction ability on par with IFM. It is based on the distance to the nearest occupied patch and not the closest habitat. It is also preferable to use, due to the minimal need for data, only requiring presence/absence data and

coordinates. The present study uses the NSi model, because of its prediction ability and minimal need for data.

2.5 Statistical analysis

The statistical analyses were done in R (version 3.6.3; R Development Core Team, 2021). 986 stones were surveyed. One record was removed due to a fieldwork error. The analyses are therefore based on 985 gravestones. The surface area of the gravestone was calculated with the width, height, and length measurements. The age of the gravestones was calculated based on the last and first engraving. The age variable used in aim 2 is based on the first inscription. The age variable in aims 3 and 4 is based on the last inscription, due to the cleaning process undertaken with each engraving of the gravestone by stonemasons. An alpha level of 0.05 was considered statistically significant.

2.5.1 Gravestone fashion

A Wilcoxon signed-rank test was used to assess if there was a significant difference in the proportion of rough and smooth textured gravestones through the years (aim 2), by testing if the gravestone age differed significantly between rough and smooth textured gravestones. Six records were removed because they contained missing values. The dependent variable age did not meet the parametric assumption of a t-test. Therefore, the non-parametric equivalent was used.

2.5.2 Colonization probability

Logistic regression was used to assess the probability of colonization at the churchyard (aim 3). Ten records were removed due to missing data, resulting in 879 absent and 96 present records. The dependent variable is occupied, with distance to the nearest occupied gravestone, gravestone age, texture of the gravestone, and surface area of the gravestone as the independent variables. Several models with different combinations of the explanatory variables, including a binomial generalized linear model (GLM) were tested. In addition, a null model was tested for comparison. The Akaike Information Criterion, corrected for small sample sizes (AICc) was used to assess the different models. The best model was the model with all variables, followed by a model with surface area removed. The difference in AICc was <2 between the models. Therefore, the more parsimonious model with the variable surface area removed was chosen

(Arnold, 2010). Model validation showed that the numeric independent variables did not have a linear relationship with the log odds. The variables distance and age were thus log-transformed and the following model was chosen (Table 2). The package MuMIn (Barton, 2020) was used for model selection.

2.5.3 Assessment of species abundance

A negative binomial GLM was used to explain the abundance of *X. loxodes* on the occupied gravestones at the churchyard (aim 4). The relationship between the dependent variable number of thalli and the independent variables distance to the nearest occupied gravestone, gravestone age, texture of the gravestone, and surface area of the gravestone was assessed. One record was removed due to missing data. A preliminary Poisson GLM was implemented due to the dependent variable being count data. However, an overdispersion (dispersion statistic: 13.39) of the data was found and the model was therefore replaced with a negative binomial GLM. Several models were assessed with different combinations of the explanatory variables. In addition, a null model was tested for comparison. The AICc was used to assess the different models. Model M7 with the explanatory variables distance, age and texture was the best model, followed by models M8 (distance and texture), M2 (distance and age), and M4 (distance, age, texture, and surface area; Table 5). There was a difference of <2 in AICc between the first three models in the table. Therefore, the second and third model due to being more parsimonious were preferred (Arnold, 2010). The packages used in the analysis were MASS (Venables & Ripley, 2002) for fitting the negative binomial model, AER (Kleiber & Zeileis, 2008) to calculate the dispersion of the best performing Poisson model, and MuMIn (Barton, 2020) for model selection.

3.0 Results

Of the 985 standing gravestones registered, *X. loxodes* was found on 97 (Figure 4). Twelve stones displayed a percentage coverage above 10%, including 3 above 20%. There were 630 individual thalli on rough gravestones and 19 on smooth textured gravestones. On the east-facing wall surrounding the churchyard, 27 individual thalli were found. No occurrences of apothecia were observed at Mære churchyard. The time series of the gravestones range from 1900 to 2021 based on the last engraving, and from 1905 to 2012 for the occupied stones.



Figure 4 The spatial distribution of *X. loxodes* at Mære churchyard. The white points are occupied gravestones scaled relative to the number of thalli per gravestone. The grey points are *X. loxodes* individuals found on the wall scaled relative to its thallus size (own photo).

3.1 Gravestone fashion

During fieldwork 562 rough and 423 smooth textured stones were registered. There was a statistically significant difference between the age of rough (median: 51, mean: 53.01) and smooth textured stones (median: 39, mean: 40.52; Wilcoxon signed-rank test, $w = 159635$, $p\text{-value} = <0.001$). The higher age of rough than smooth gravestones and the age distribution of rough and smooth gravestones indicate that the number of smooth stones seems to increase (Figure 5).

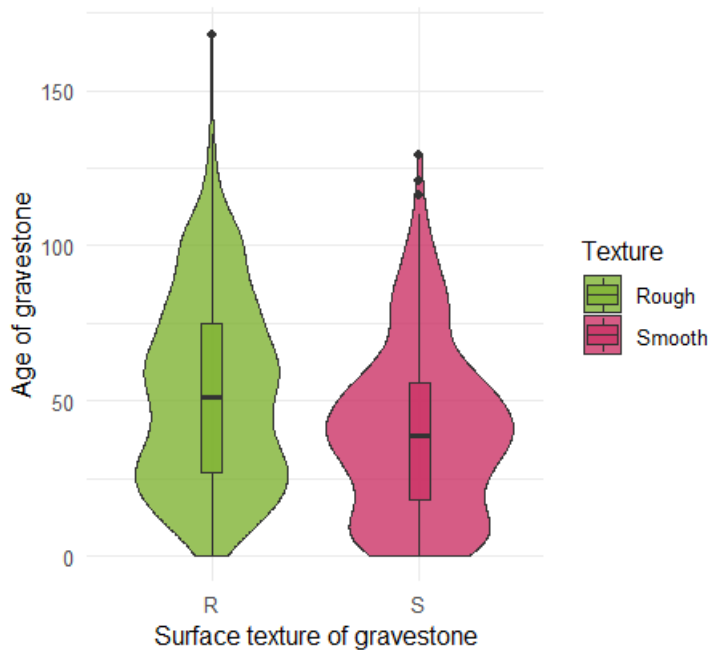


Figure 5 A violin plot of the age of gravestones divided by their surface texture. The line in the boxplot inside the violin, is the median. The gravestone age is based on the first inscription of the gravestone.

3.2 Colonization probability

Based on all standing gravestones the chance of colonization was influenced by the variables distance ($p\text{-value} <0.001$), gravestone age ($p\text{-value} <0.001$) and texture ($p\text{-value} <0.001$; Table 1). The colonization probability decays exponentially (estimate β : -1.354) with increasing distance from the closest occupied gravestone. It increases (estimate β : 1.106) with gravestone age. Smooth textured stones are significantly more difficult to colonize than rough textured stones (estimate β : -1.757). The predicted probability is only above 25 % for any variable, when the distance to the nearest occupied gravestone is small and when gravestones have a high age and a rough surface texture (Figure 6).

Table 1 Output of the logistic regression model. β : estimate, SE: standard error, z-value: test statistic. The variables distance and age are log transformed. The smooth texture is compared to the reference level rough texture in the variable texture, which is not shown in this table.

| | β | SE | z-value | p-value |
|----------------|---------|-------|---------|---------|
| Intercept | -3.901 | 0.763 | -5.111 | <0.001 |
| log(Distance) | -1.354 | 0.195 | -6.958 | <0.001 |
| log(Age) | 1.106 | 0.197 | 5.561 | <0.001 |
| Smooth texture | -1.757 | 0.395 | -4.453 | <0.001 |

Table 2 Model selection table after log transformation, from the MuMIn package. Df = degrees of freedom. AICc = Akaike Information Criterion. $\Delta AICc$ = the difference in AICc value between the best model and the following models. AICcw = the model weight.

| Candidate model | log (Distance) | log (Age) | Texture | Surface area | df | AICc | $\Delta AICc$ | AICcw |
|-----------------|----------------|-----------|---------|--------------|----|-------|---------------|-------|
| M4a | ✓ | ✓ | ✓ | | 4 | 452.7 | 0.00 | 1 |
| M0 | | | | | 1 | 630.1 | 177.47 | 0 |

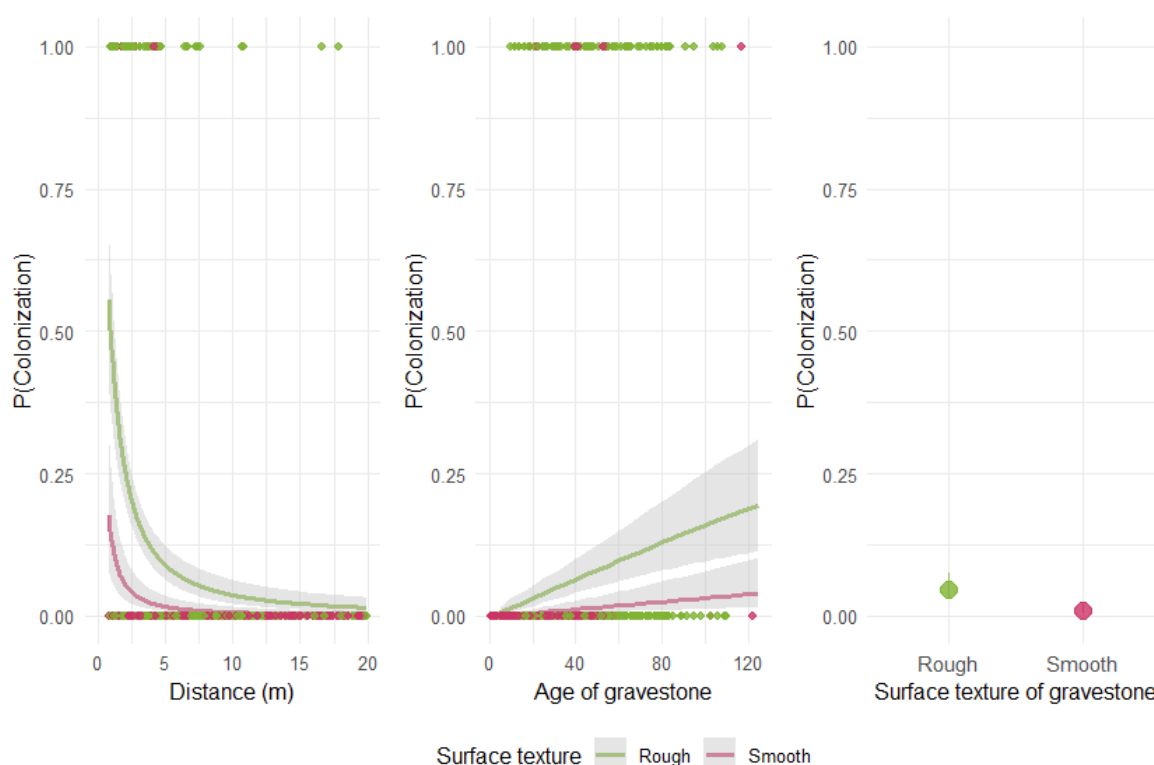


Figure 6 Predicted colonization probability on all gravestones ($n=975$) based on distance, age and surface texture of the gravestone. The grey polygons and error bars: the 95% confidence interval. The lines and points: the predicted mean. $P(\text{Colonization})$: the probability of colonization. The points in the bottom and top part of the figure: the observed values. The variables distance and age are log-transformed.

3.3 Abundance of *X. loxodes*

The models that included the variables distance and texture (M8; ΔAICc : 1.68) and distance and age (M2; ΔAICc : 1.86) were more parsimonious and outperformed the model that included all three variables (ΔAICc : 0.00; Table 5). Distance is an important predictor of the number of thalli; since it is included in all the best models during model selection (Table 5) and is statistically significant for the two top-performing models that were chosen (Table 3, Table 4). With increasing distance, the number of thalli exponentially decays (M8 estimate β : -0.177, M2 estimate β : -0.159; Figure 7, Table 3, Table 4).

Table 3 Output of the negative binomial model (M8). β : estimate, SE: standard error, Z-value: test statistic. Smooth texture is compared to the reference level rough texture in the variable texture, which is not shown in this table.

| | β | SE | z-value | p-value |
|----------------|---------|-------|---------|---------|
| Intercept | 2.432 | 0.189 | 12.859 | <0.001 |
| Distance | -0.177 | 0.051 | -3.464 | <0.001 |
| Smooth texture | -1.146 | 0.453 | -2.529 | 0.011 |

Table 4 Output of the negative binomial model (M2). β : estimate, SE: standard error, z-value: test statistic.

| | β | SE | z-value | p-value |
|-----------|---------|-------|---------|---------|
| Intercept | 1.671 | 0.301 | 5.556 | <0.001 |
| Distance | -0.159 | 0.517 | -3.091 | 0.002 |
| Age | 0.012 | 0.005 | 2.641 | 0.008 |

The variables age and texture affect the number of thalli, but it is not possible to infer which variable is more crucial, due to the conflicting models having a similar AICc (M2 and M8; Table 5). The number of thalli increases with the gravestone age (estimate β : 0.012; Figure 8, Table 4). In addition, the number of thalli is predicted to be lower for smooth textured gravestones compared to rough textured ones (estimate β : -1.146; Figure 8, Table 3). The surface area of the gravestone has only a negligible effect on the abundance of *X. loxodes* and is not included in the three top models (Table 5).

Table 5 Model selection table from the MuMIn package. Df = degrees of freedom. AICc = Akaike Information Criterion. Δ AICc = the difference in AICc value between the best model and the following models. AICcw = the model weight.

| Candidate model | Distance | Age | Texture | Surface area | df | AICc | Δ AICc | AICcw |
|-----------------|----------|-----|---------|--------------|----|-------|---------------|-------|
| M7 | ✓ | ✓ | ✓ | | 5 | 559.6 | 0.00 | 0.382 |
| M8 | ✓ | | ✓ | | 4 | 561.2 | 1.68 | 0.165 |
| M2 | ✓ | ✓ | | | 4 | 561.4 | 1.86 | 0.150 |
| M4 | ✓ | ✓ | ✓ | ✓ | 6 | 561.7 | 2.13 | 0.132 |
| M6 | ✓ | | ✓ | ✓ | 5 | 563.4 | 3.86 | 0.055 |
| M3 | ✓ | ✓ | | ✓ | 5 | 563.5 | 3.96 | 0.053 |
| M1 | ✓ | | | | 3 | 564.4 | 4.83 | 0.034 |
| M5 | ✓ | | | ✓ | 4 | 566.5 | 6.99 | 0.012 |
| M11 | | ✓ | | | 3 | 568.1 | 8.52 | 0.005 |
| M9 | | ✓ | ✓ | ✓ | 5 | 568.6 | 9.00 | 0.004 |
| M10 | | ✓ | | ✓ | 4 | 569.5 | 9.99 | 0.003 |
| M12 | | | ✓ | | 3 | 569.9 | 10.34 | 0.002 |
| M14 | | | ✓ | ✓ | 4 | 571.5 | 11.94 | 0.001 |
| M0 | | | | | 2 | 572.3 | 12.75 | 0.001 |
| M13 | | | | ✓ | 3 | 574.0 | 14.41 | 0.000 |

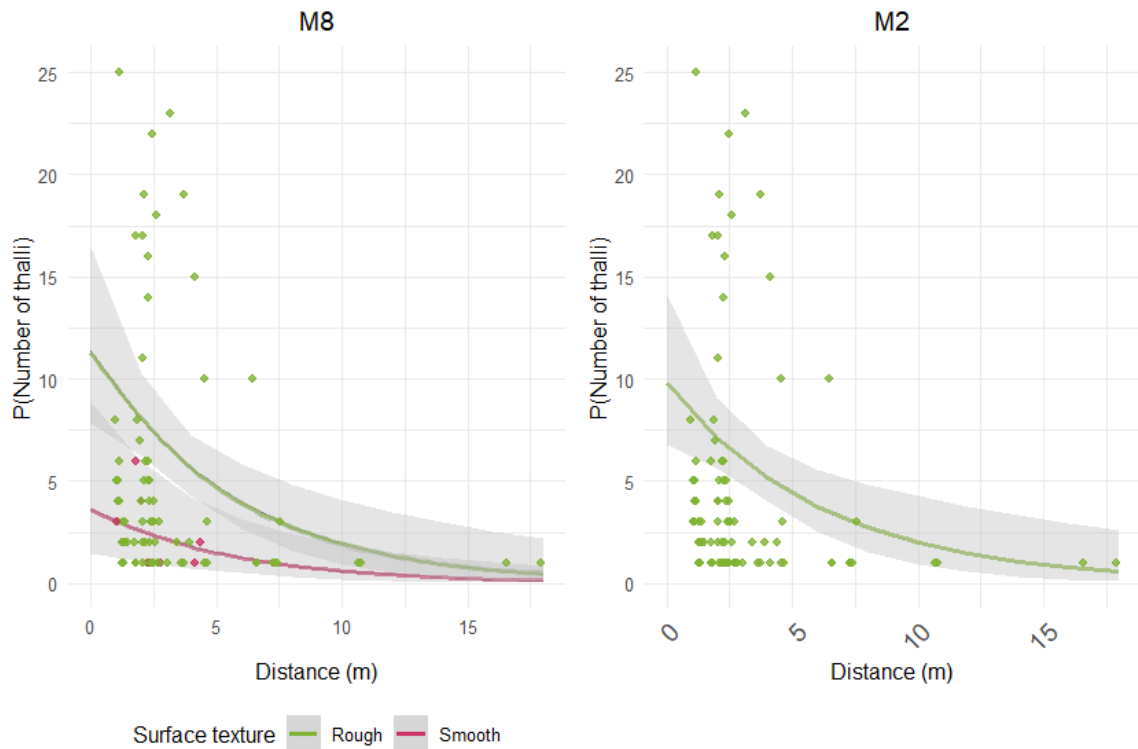


Figure 7 Predicted number of thalli on a gravestone based on distance to the nearest occupied gravestone in model 8 (left) and 2 (right). $P(\text{Number of thalli})$: the predicted number of thalli. The grey polygons: the 95% confidence interval. The lines: the predicted mean. The points: observed values.

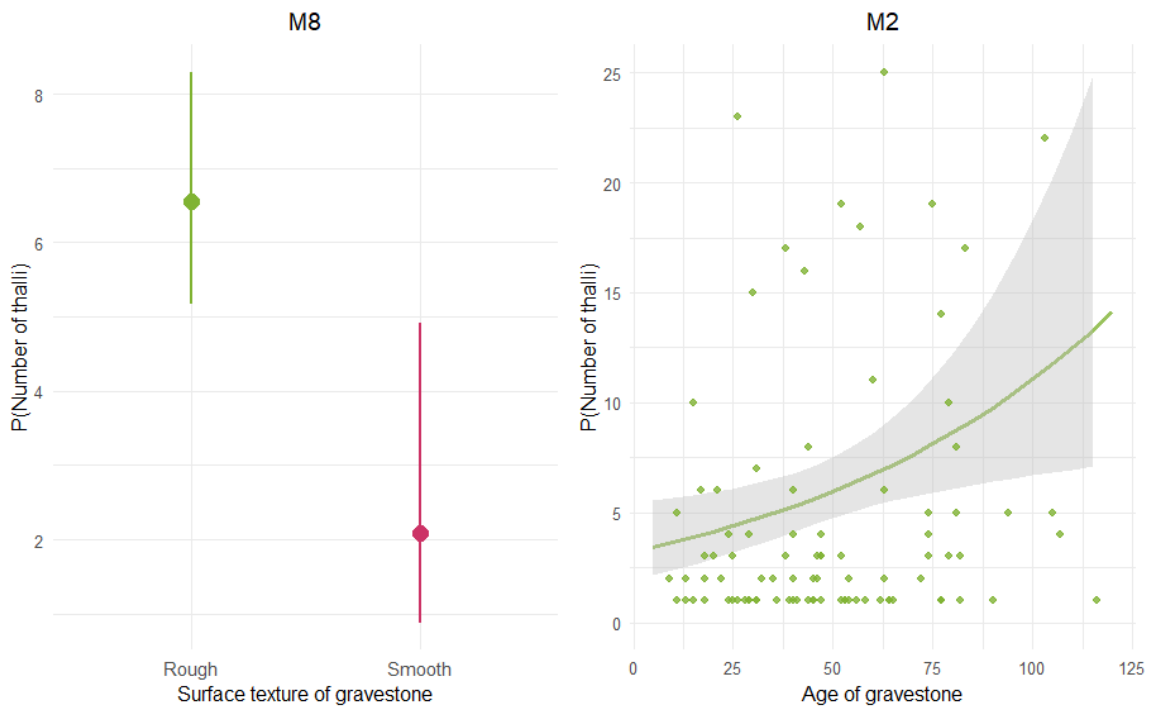


Figure 8 Predicted number of thalli on a gravestone based on surface texture of the gravestone in model 8 (left) and age of gravestone in model 2 (right). $P(\text{Number of thalli})$: the predicted number of thalli. In figure M8 (left) the points: the mean; the lines: the 95% confidence interval. In figure M2 (right) the line: the mean; the grey polygons: the 95% confidence interval; the green points: the observed values.

4.0 Discussion

The probability of finding *X. loxodes* on a gravestone was affected by distance to the nearest occupied patch, age of the gravestone, and surface texture of the gravestone. The abundance of *X. loxodes* was also affected by the distance to the nearest patch, but the effect of age and surface texture of the gravestone was less clear. There was a significant difference between the proportion of rough and smooth textured gravestones through time, which could be important for the establishment of lichens on gravestones in the future.

4.1 Connectivity

The reproductive strategy of sessile species and the spatial configuration of the landscape can have a significant impact on the local and regional distribution of sessile species. To successfully colonize or recolonize a patch, i.e., gravestones in the present study, the lichen must disperse propagules to the patch and be able to establish a new thallus there. The gravestones in churchyards and cemeteries usually have a uniform spatial pattern. Due to minimal research on this topic, it is unclear how distance between patches affects biodiversity there. Following the recommendation of Prugh (2009), distance to the nearest occupied patch was used as a measure of connectivity. I found a significant effect on both the colonization probability and abundance of *X. loxodes* (Figure 6, Figure 7). Both decreased with increasing distance to the nearest occupied stone. This result concurs with the only other study of isolation by distance of lichens in churchyards and cemeteries, in which the phenomenon was tested both spatially and temporally by Warren (2003). One could therefore conclude that *X. loxodes* is limited by dispersal and experience low connectivity between patches. This shows that the nearest source model also can apply to this habitat. However, other distance connectivity measures could have been on par with the nearest source metric or better. One example is distance to all occupied patches (Hanski, 1999). In the study by Warren (2003), only one, *Candelariella vitellina*, of two studied lichen species experienced isolation by distance in one out of the three cemeteries. Both species dispersed vegetatively, but *C. vitellina* had a limited amount of ideal gravestone habitat available compared to the other species. The spatial configuration of the substrate might therefore have played a larger role in the connectivity between patches for this species. Most studies on connectivity of sessile species are concentrated on epiphyte species in forests where numerous species experience isolation by distance (e.g. Johansson & Ehrlén, 2003; Johansson et al., 2012; Snäll et al., 2005). Dispersal can even be limiting for small-spored fungi in forests (Jönsson et al., 2008). However, the

observation that solely one lichen experienced isolation by distance in the study of Warren (2003) indicates that other factors also influence the distribution pattern in churchyards and cemeteries. This is confirmed in the present study since the model with merely the variable distance included shows a reduced performance compared to models that include gravestone characteristics (Table 5). Thus, factors influencing the establishment of a lichen on an ideal substrate may also affect the distribution, despite dispersal being the main limiting factor. This is also the case for epiphytic lichens at local scales in other habitats, where tree species and tree size influenced the presence of lichens at tree level (Johansson & Ehrlén, 2003).

In addition to distance, increased patch size is often found to be positively correlated with species richness (Hanski, 1999; MacArthur & Wilson, 1967). In the present study gravestone surface area, did not have a significant effect on either the abundance or colonization probability of *X. loxodes* at Mære churchyard (Table 2, Table 5). Tree size, independent of age, is assumed to be important for the colonization of lichens, due to larger surface area and coarser bark. The probability of propagules attaching to the surface may therefore be higher for larger trees (Gu et al., 2001). However, gravestones in general seem to have little variation in size. This could be a possible cause for the absent effect of patch size in the present study. While patch size is an important variable for the distribution of species in other habitats (e.g. Johansson & Ehrlén, 2003), the inclusion of this variable does not seem to be crucial for the analysis of the distribution of species in churchyards and cemeteries.

4.2 Gravestone characteristics

In addition to distance between occupied gravestones, the variables age and texture of the gravestones influence the observed distribution pattern. It is thought that gravestones are ideal habitat patches from when they are erected, in contrast to trees that only become suitable after a certain time (Johansson et al., 2012). Therefore, the higher the number of years since erection or last cleaning of the stone, the higher is the probability of colonization. This is also indicated in the present study. If the distance to another occupied patch is low, it is only a question of time before colonization occurs (Gjerde et al., 2012). In addition, colonization probability was positively affected by the rough texture of the gravestones, and negatively affected by the smooth polished texture (Figure 6). This could be compared with the variables tree age and tree texture to some degree, which influence the occurrence of lichens significantly (Ranius et al., 2008). The bark of most trees is correlated with tree size and will increase in roughness and

crevice depth with age (e.g. Ferrenberg et al., 2014). The roughness of stones however is decided by the manufacturer and remains more or less constant after the gravestone has been placed. The preference for rough-barked trees is however shown to be species-specific. The results of Sillett et al. (2000) did not support the assumption that the roughness of the substrate is important for the occurrence of the species. Specifically, the macrolichen *Lobaria oregana* was found in both young forests where the bark is smooth and in old forests where the bark is rougher. However, Ranius et al. (2008) showed that crustose lichens depend on the deep bark crevices. According to the authors, the underlying cause behind the association is not known but is assumed to be the microclimate or the physical and chemical characteristics of bark. Bark is however a more dynamic substrate and has some different characteristics than the surface of stones. The constant textured state of gravestones is important since the colonization of highly polished stones is assumed to be slower and more impaired (Seaward, 1977). This is in line with the assumption of Miller et al. (2012) that rough stone surfaces are an important factor in biological establishment. This also seems to apply to lichen establishment on gravestones based on my results. It could however also be other factors among the geochemical and physical differences among stone types (Adamo & Violante, 2000) that influence colonization.

Both age and texture affect the abundance of *X. loxodes*. However, age and texture were each a part of competing models, and it is therefore not possible to conclude which is more important (Table 5). The abundance of *X. loxodes* does increase with the increasing age of the gravestone (Figure 8). The small increase could be due to the thalli having more time to grow vegetatively. As lichens have variable life spans, from a few months to decades (Schöller & Büdel, 1997), the time to develop and grow is important. On the other hand, *X. loxodes* might be a good colonizer as soon as it is established on a gravestone. It then reproduces fast and the abundance on the stone accumulates quickly (Leger & Forister, 2009). Consequently, the age of the gravestone would not be as important. The presumed ability of rough stones to act as anchoring points for propagules may also lose its effect after a stone has been colonized. Other factors, e.g., competition, environmental variables, and stone characteristics, might take over. Rock types are not considered an important factor for the distribution pattern of *X. loxodes*, due to the species preferring acidic rocks (Stenroos et al., 2021), which the gravestones at Mære church mainly consist of. Additionally, it is expected that succession occurs on gravestones exhibiting an increased species richness (Hill, 1994). The weathering of stones results in a change of porosity and pH that might correlate with belatedly appearing lichens. The study by Hill (1994) analyzed calcareous stones and hence this remains to be tested on acidic stones.

How *X. loxodes* behaves regarding succession and competitive ability also remains to be assessed.

4.3 Gravestone fashion

Lastly, churchyards and cemeteries are human-made habitats, and the human influence must be considered. Gravestones are made of a variety of stone types ideal for colonization by lichens like *X. loxodes*. As stated before, one factor suspected to be important is the roughness of the stones. It is thought that rougher stones have better anchoring points for biological colonization, compared with polished stones (Miller et al., 2012) The popularity of certain gravestones can change through time. The results indicate a significant increase in the use of smooth textured gravestones with time (Figure 5). The increase of smooth textured stones could affect the future abundance and colonization probability of lichens like *X. loxodes* negatively. The effect is already indicated with the finding of 630 thalli on rough stones, compared to 19 on smooth stones at Mære. My results show that the presence/absence of *X. loxodes* is negatively affected by smoother stones, which gives credence to the assumption of Miller et al. (2012) that smoother stones are poorer substrates for colonization. The human element in churchyards and cemeteries should thus not be forgotten, because the choice of gravestone can affect the biodiversity found there.

5.0 Conclusion

Based on the results of the present study, connectivity has a significant effect on the spatial distribution of *X. loxodes* in the churchyard. Patch size does not matter, but stone characteristics do. This indicates that *X. loxodes* is limited by dispersal and that the species is a good colonizer when it has managed to establish itself on a stone. Since the abundance at Mære churchyard was relatively large, a larger area of occupancy could be found around the churchyard by *X. loxodes* if surveyed. In the future, a more extensive search of old churchyards and cemeteries with an unknown amount of biodiversity should be undertaken. When finding threatened species, their population viability should be assessed with a metapopulation approach. As shown in this study, there should be a thorough search on which factors affect the colonization of gravestones, as they can be species-specific.

References

- Adamo, P., & Violante, P. (2000). Weathering of rocks and neogenesis of minerals associated with lichen activity. *Applied Clay Science*, 16(5), 229-256.
[https://doi.org/10.1016/S0169-1317\(99\)00056-3](https://doi.org/10.1016/S0169-1317(99)00056-3)
- Andren, H. (1994). Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos*, 71(3), 355-366.
<https://doi.org/10.2307/3545823>
- Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *The Journal of wildlife management*, 74(6), 1175-1178.
<https://doi.org/10.2193/2009-367>
- Artdatabanken. (n.d.). *Registrerte observasjoner: Klubbeskjærgårdslav* Artsdatabanken.
<https://artsdatabanken.no/Taxon/Xanthoparmelia%20loxodes/145207>
- Barrett, G. W., & Barrett, T. L. (2001). Cemeteries as Repositories of Natural and Cultural Diversity. *Conservation Biology*, 15(6), 1820-1824. <https://doi.org/10.1046/j.1523-1739.2001.00410.x>
- Barton, K. (2020). *MuMIn: Multi-Model Inference*. In <https://CRAN.R-project.org/package=MuMIn>
- Biedermann, R. (2005). Incidence and population dynamics of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Ecography*, 28(5), 673-681.
<https://doi.org/10.1111/j.2005.0906-7590.04217.x>
- Buchholz, S., Blick, T., Hannig, K., Kowarik, I., Lemke, A., Otte, V., Sharon, J., Schönhofer, A., Teige, T., von der Lippe, M., & Seitz, B. (2016). Biological richness of a large urban cemetery in Berlin. Results of a multi-taxon approach. *Biodivers Data J*, 4(1), e7057-e7057. <https://doi.org/10.3897/BDJ.4.e7057>
- Crooks, K. R., & Sanjayan, M. A. (2006). *Connectivity conservation* (Vol. 14). Cambridge University Press.
- Dearborn, D. C., & Kark, S. (2010). Motivations for Conserving Urban Biodiversity. *Conserv Biol*, 24(2), 432-440. <https://doi.org/10.1111/j.1523-1739.2009.01328.x>
- Dennis, E. (1993). The Living Churchyard - Sanctuaries for Wildlife. *British Wildlife*, 4, 230 - 241.
- Ferrenberg, S., Mitton, J. B., & Jones, H. (2014). Smooth bark surfaces can defend trees against insect attack: resurrecting a 'slippery' hypothesis. *Functional ecology*, 28(4), 837-845. <https://doi.org/10.1111/1365-2435.12228>

- Gilbert, O. L. (1991). *The Ecology of Urban Habitats*. Dordrecht: Springer Netherlands.
- Gjerde, I., Blom, H. H., Lindblom, L., Sætersdal, M., & Schei, F. H. (2012). Community assembly in epiphytic lichens in early stages of colonization. *Ecology*, *93*(4), 749-759. <https://doi.org/10.1890/11-1018.1>
- Gu, W.-D., Kuusinen, M., Konttinen, T., & Hanski, I. (2001). Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin boreal forests. *Ecography*, *24*(2), 139-150. <https://doi.org/10.1034/j.1600-0587.2001.240204.x>
- Halda, J. P., Janeček, V. P., & Horák, J. (2020). Important part of urban biodiversity: Lichens in cemeteries are influenced by the settlement hierarchy and substrate quality. *Urban forestry & urban greening*, *53*, 126742. <https://doi.org/10.1016/j.ufug.2020.126742>
- Hanski, I. (1998). Metapopulation dynamics. *Nature (London)*, *396*(6706), 41-49. <https://doi.org/10.1038/23876>
- Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.
- Hanski, I., Kuussaari, M., & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology (Durham)*, *75*(3), 747-762. <https://doi.org/10.2307/1941732>
- Hill, D. (1994). The Succession of Lichens on Gravestones: a Preliminary Investigation. *Cryptogamic Botany*, *4*, 179-186.
- Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., Lyon, B. N., Metzger, G. A., Olandese, M. L., Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C., & Williams, S. E. (2007). Does size matter for dispersal distance? *Global ecology and biogeography*, *16*(4), 415-425. <https://doi.org/10.1111/j.1466-8238.2007.00312.x>
- Johansson, P., & Ehrlén, J. (2003). Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *The Journal of ecology*, *91*(2), 213-221. <https://doi.org/10.1046/j.1365-2745.2003.t01-1-00754.x>
- Johansson, V., Ranius, T., & Snäll, T. (2012). Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology*, *93*(2), 235-241. <https://doi.org/10.1890/11-0760.1>
- Jönsson, M. T., Edman, M., & Jonsson, B. G. (2008). Colonization and Extinction Patterns of Wood-Decaying Fungi in a Boreal Old-Growth *Picea abies* Forest. *Journal of Ecology*, *96*(5), 1065-1075. <https://doi.org/10.1111/j.1365-2745.2008.01411.x>
- Kendal, D., Zeeman, B. J., Ikin, K., Lunt, I. D., McDonnell, M. J., Farrar, A., Pearce, L. M., & Morgan, J. W. (2017). The importance of small urban reserves for plant

- conservation. *Biological conservation*, 213, 146-153.
<https://doi.org/10.1016/j.biocon.2017.07.007>
- Kleiber, C., & Zeileis, A. (2008). *Applied econometrics with R*. Springer.
- Klimaservicesenter, N. (2021). *Klimanormaler*. Norsk Klimaservicesenter. Retrieved 27.04 from <https://klimaservicesenter.no/kss/vrdata/normaler#nye-normaler-for-stasjoner>
- Kowarik, I., Buchholz, S., von der Lippe, M., & Seitz, B. (2016). Biodiversity functions of urban cemeteries: Evidence from one of the largest Jewish cemeteries in Europe. *Urban forestry & urban greening*, 19, 68-78.
<https://doi.org/10.1016/j.ufug.2016.06.023>
- Leger, E. A., & Forister, M. L. (2009). Colonization, abundance, and geographic range size of gravestone lichens. *Basic and applied ecology*, 10(3), 279-287.
<https://doi.org/10.1016/j.baae.2008.04.001>
- Levins, R. (1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Entomological Society of America*, 15, 237-240.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography* (Vol. 1). Princeton University Press.
- Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Ak?Akaya, H. R., Leader-Williams, N., Milner-Gulland, E. J., & Stuart, S. N. (2008). Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. *Conserv Biol*, 22(6), 1424-1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>
- McBarron, E. J., Benson, D., & Doherty, M. D. (1988). The botany of old cemeteries. *Cunninghamia*, 2, 97 - 105.
- Miller, A. Z., Sanmartín, P., Pereira-Pardo, L., Dionísio, A., Saiz-Jimenez, C., Macedo, M. F., & Prieto, B. (2012). Bioreceptivity of building stones: A review. *Sci Total Environ*, 426, 1-12. <https://doi.org/10.1016/j.scitotenv.2012.03.026>
- Moen, A. (1998). *Vegetasjon*. Norges geografiske oppmåling.
- Moilanen, A., & Hanski, I. (2001). On the use of connectivity measures in spatial ecology. *Oikos*, 95(1), 147-151. <https://doi.org/10.1034/j.1600-0706.2001.950116.x>
- Moilanen, A., & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology (Durham)*, 83(4), 1131-1145. <https://doi.org/10.2307/3071919>
- Morgan, N. (2016). Gravestone geology. *Geology Today*, 32(4), 154-159.
<https://doi.org/10.1111/gto.12146>
- Nordberg, H. M., & Mære, s. (1989). *Mære kyrkje 800 år*. Mære sokneråd.

- Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T., & Ovaskainen, O. (2014). Do small spores disperse further than large spores? *Ecology*, *95*(6), 1612-1621. <https://doi.org/10.1890/13-0877.1>
- Öckinger, E., Niklasson, M., & Nilsson, S. G. (2005). Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodiversity and conservation*, *14*(3), 759-773. <https://doi.org/10.1007/s10531-004-4535-x>
- Owczarek-Kościelniak, M., Krzewicka, B., Piątek, J., Kołodziejczyk, Ł. M., & Kapusta, P. (2020). Is there a link between the biological colonization of the gravestone and its deterioration? *International biodeterioration & biodegradation*, *148*, 104879. <https://doi.org/10.1016/j.ibiod.2019.104879>
- Prugh, L. R. (2009). An Evaluation of Patch Connectivity Measures. *Ecol Appl*, *19*(5), 1300-1310. <https://doi.org/10.1890/08-1524.1>
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of Habitat Area and Isolation on Fragmented Animal Populations. *Proc Natl Acad Sci U S A*, *105*(52), 20770-20775. <https://doi.org/10.1073/pnas.0806080105>
- Purvis, O. W. (2010). *Lichens* ([Updated]. ed.). Natural History Museum.
- R Development Core Team. (2021). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ranius, T., Johansson, P., Berg, N., & Niklasson, M. (2008). The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of vegetation science*, *19*(5), 653-662. <https://doi.org/10.3170/2008-8-18433>
- Schöller, H., & Büdel, B. (1997). *Flechten : Geschichte, Biologie, Systematik, Ökologie, Naturschutz und kulturelle Bedeutung* (Vol. 27). Kramer.
- Schumann, W., Eisenbeiss, H., & Tollefsrud, J. I. (2000). *Norsk steinhåndbok* (2. rev. utg. ed.). Aschehoug.
- Seaward, M. R. D. (1977). *Lichen ecology*. Academic press.
- Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R., & Ruchty, A. (2000). Dispersal Limitations of Epiphytic Lichens Result in Species Dependent on Old-Growth Forests. *Ecological applications*, *10*(3), 789-799. [https://doi.org/10.1890/1051-0761\(2000\)010\[0789:DLOELR\]2.0.CO2](https://doi.org/10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO2)
- Smith, C. W., Smith, C. W., & British Lichen, S. (2009). *The lichens of Great Britain and Ireland* ([Rev.] / edited by C.W. Smith ... [et. al]. ed.). British Lichen Society.

- Snäll, T., Ehrlen, J., & Rydin, H. (2005). Colonization-Extinction Dynamics of an Epiphyte Metapopulation in a Dynamic Landscape. *Ecology (Durham)*, 86(1), 106-115.
<https://doi.org/10.1890/04-0531>
- Snäll, T., Hagström, A., Rudolphi, J., & Rydin, H. (2004). Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales - importance of past landscape structure, connectivity and local conditions. *Ecography*, 27(6), 757-766.
<https://doi.org/10.1111/j.0906-7590.2004.04026.x>
- Snäll, T., Pennanen, J., Kivistö, L., & Hanski, I. (2005). Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos*, 109(2), 209-222.
<https://doi.org/10.1111/j.0030-1299.2005.13616.x>
- Stenroos, S., Velmala, S., Pykälä, J., & Ahti, T. (2021). *Lichens of Finland* (2 ed., Vol. 30). Naturcentrum AB.
- Tischendorf, L., & Fahrig, L. (2001). On the use of connectivity measures in spatial ecology. Authors' reply. *Oikos*, 95(1), 147-155.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.
- Warren, J. (2003). Isolation by distance in the crustose lichens *Candelariella vitellina* and *Placynthium nigrum* colonising gravestones in northeast Scotland. *Biodiversity and conservation*, 12(2), 217-224. <https://doi.org/10.1023/A:1021982826652>
- Wirth, V. (2013). *Die Flechten Deutschlands : Bd. 2* (Vol. Bd. 2). Ulmer.
- Yilmaz, H., Kusak, B., & Akkemik, U. (2018). The role of Aşiyân Cemetery (İstanbul) as a green urban space from an ecological perspective and its importance in urban plant diversity. *Urban forestry & urban greening*, 33, 92-98.
<https://doi.org/10.1016/j.ufug.2017.10.011>