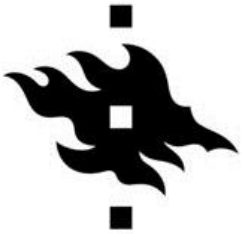
Post-harvest natural regeneration and vegetation dynamics across forest gaps in Central Finland

Thesis submitted for a M.Sc. degree in Forest Sciences and Business



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ABSTRACT

The creation of forest gaps in disturbance emulation forestry alters local environmental conditions, which causes variability in natural seedling regeneration. Understory vegetation plays an important role in early seedling regeneration success and is sensitive to variations in topography and resource availability. Its analysis can uncover the finer-scale impacts of gap characteristics and competition on the patterns of tree regeneration.

The objective of this study was to examine the impact of gap characteristics on patterns of natural vegetation and tree seedling regeneration 5 years post-harvest across 18 gaps in Norway spruce (*Picea abies* (L.) Karst.) dominated forests of Central Finland. Gap characteristics included distance from edge (into residual forest and gap interior), cardinal position in the gap (N, S, E or W), microsite type and dominant topography. All seedlings (≤5m) were counted and measured on 1m^2 plots situated along linear strips (2 for each N-S and E-W orientations). On these same plots, vegetation and microsite types were assessed by percent cover for several key categories.

Results show that distance from gap edge was the most influential gap characteristic, especially in the ±10m zone. The 0–15m zone inside the gap supported the greatest abundance of seedlings, as well as the highest diversity of both vegetation types and seedling species. The edge zone inside the forest supported shade-tolerant species (dwarf shrubs, mosses). Gap centers (~15m+) supported shade-intolerant species (grasses, shrubs, herbs), creating a highly competitive growing environment. The position within the gap was also an influential characteristic. The N gap positions showed the most statistically significant difference from the others; they had fewer birch seedlings, a greater percent cover of grasses and dwarf shrubs, and a smaller percent cover of ferns. This effect was generally more pronounced in the gap interior.

The results of this study support that natural regeneration of seedlings in gaps is quite variable. The mean number of seedlings per ha inside the gaps were 20 360 for Norway spruce, and 6 820 for birch spp. combined; up to 62% were germinants (≤3cm). In the 15m+ region from the gap edge towards the gap center, the mean number of seedlings per m^2 was on average ~58% smaller than for the rest of the strip. The presence and abundance of different vegetation species clearly demonstrate that distance from edge and within-gap position strongly affect resource availability and competition. The most significant gap characteristics affecting these patterns of early regeneration for Norway spruce and birch were revealed with the help of generalized additive models (GAMs). Since these gaps are in their early stages of regeneration, the future dynamics and final outcome are still fairly uncertain. However, the current mean number of seedlings inside the gaps suggests a promising potential for natural regeneration. These models point to management actions which could facilitate long-term natural regeneration in similar forest gaps.

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1. INTRODUCTION

1.1. Background

1.1.1. Forest management in a historical context

For several decades, the boreal forest of Fennoscandia has been largely managed for timber production. From the 1950s onward, the dominant approach has been clear-cut harvesting followed by single-species seeding and planting, producing a landscape dominated primarily by even-aged stands of Scots pine and Norway spruce. Although natural seeding of various shade-intolerant species occurs in these systems (e.g., birch, poplar, rowan), their cultivation has been greatly suppressed by these management approaches. These practices have limited the compositional and temporal variability at the forest stand-level, the dominant forest management unit. Consequently, the greater landscape-level structural variability has also been greatly reduced. Given that structural variability in unmanaged Fennoscandian forests typically occurs at a variety of spatial scales within the landscape (Kuuluvainen and Aakala 2011), these practices severely compromised the diversity and quality of natural forest habitats.

During the past two or so decades, evidence has grown regarding the negative impacts of even-aged approaches on forest ecosystem health (Esseen et al. 1997, Kuuluvainen 2002) and biodiversity (Hanski 2000, Auvinen et al. 2007, Raunio et al. 2008), and the number of endangered and red-listed species has increased (Kouki et al. 2001, Gärdenfors 2005, Rassi et al. 2010). As well, the role of heterogeneous forest structures in promoting species diversity has become increasingly clear (Haveri and Carey 2000, Aukema and Carey 2008). In response, a number of alternative management guidelines and best practices have been introduced. These include, but are not limited to, the retention of individual trees (dead and alive) (Gustafsson et al. 2010) and patches of trees within the clear-cut areas, along water bodies (as riparian buffers), and in ecologically valuable or sensitive habitats (Timonen et al. 2010). Notwithstanding these developments in awareness and in best practises, the dominant approach in forest management has largely remained the same.

Conventional forest management approaches (e.g., planting, mechanized thinning and harvesting, and fertilization) and pulpwood processing generally require substantial financial and energy inputs. The international demand for paper has significantly diminished during the past decades. Since these products had long been an important component of the pulp and

paper industries in Fennoscandia, these changes have triggered market instability in these regions. However, in recent years China's population boom has fueled a significant demand for toilet paper, reviving the pulp and paper industry in Fennoscandia. Nevertheless, fluctuating demand paired with the rising cost of oil and gas has rendered the industry more unstable and in some cases less profitable.

Conversely, the economic importance of nature tourism in Fennoscandia has experienced significant growth. Nature tourism, along with the growing interest in preserving recreational and other non-timber values of forests, is contributing to a rising interest in alternative forest management approaches (Valkonen et al. 2010, Pukkala et al. 2011). Accordingly, recent studies have revealed an important decrease in societal support for clear-cutting techniques and a simultaneous increased interest in alternative forest management practices (Valkeapää et al. 2009, Kumela and Hänninen 2011).

Internationally, forest management priorities have increasingly broadened beyond a focus on timber values alone, now often reflecting multiple short- and long-term values pertaining to biodiversity conservation, resilience and adaptability in the face of local and global change, a greater array of economic goods obtained from the forest (often termed non-timber forest products, or NTFPs), and the provision of various ecosystem services and opportunities for recreation (Spence 2001, Drever et al. 2006, Puettmann et al. 2009, Miina et al. 2010, Messier et al. 2013). This requires a shift from managing forests at the stand scale to considering multiple factors within the landscape scale. One forest management approach which has demonstrated potential for providing multiple benefits is natural disturbance emulation, or NDE (Attiwill 1994, Bergeron et al. 2002, Long 2009). NDE mimics natural tree mortality patterns by employing a diversity of timber harvesting techniques at various temporal and spatial scales (Gauthier et al. 2009). These harvesting patterns are designed based on knowledge of historical disturbance patterns typical of the type of forest being managed.

1.1.2. Natural disturbance dynamics in the boreal forest

Natural disturbances consist of biotic and abiotic agents that cause the death of trees at the individual, stand and landscape level (Keane et al. 2009); each disturbance event can affect forest areas ranging from smaller than one meter squared up to thousands of hectares.

Together, these natural disturbances alter forest structure and species composition at varied spatial and temporal scales (Forman 1995). They are an important component of boreal forest ecosystems, and their role in maintaining many ecosystem processes and functions has become increasingly well understood (Oliver 1980, Attiwill 1994, Gauthier et al. 2009, Kneeshaw et al. 2011, Kuuluvainen and Grenfell 2012).

In spruce-dominated boreal forests typical of Eurasia and Fennoscandia, natural disturbances tend to produce gap-mosaic dynamics (Kuuluvainen 1994, McCarthy 2001, Gromtsev 2002). These gaps result most frequently from repeated small-scale disturbances caused by wind, surface fires, heavy snow loads, insect outbreaks or pathogens; large-scale gap disturbances or stand-replacing events (such as wildfires, or severe storms) are much more infrequent (Sernander 1936, Liu and Hytteborn 1991, Kuuluvainen 1994, Zackrisson et al. 1995, Kuuluvainen et al. 1998a, Bergeron et al. 1999, Engelmark and Hytteborn 1999, Kuuluvainen 2002, Caron et al. 2009, Shorohova et al. 2009, Kuuluvainen and Aakala 2011) (Fig. 1).

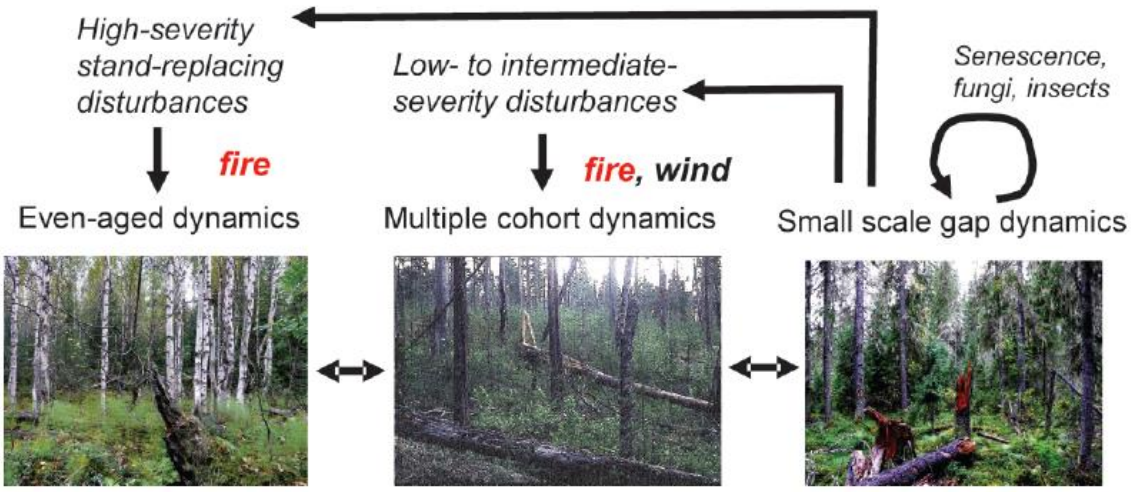


Figure 1. Boreal forest natural disturbance dynamics (Kuuluvainen 2009)

1.1.3. Natural disturbance emulation forestry

The traditional more intensive methods of forest management have created a legacy of fairly homogeneous forest landscapes, with limited structural and compositional variability. Natural disturbance emulation (NDE) is an integrated forest management approach in which the primary goal is to create landscape-scale variability through diversifying the forest harvest in terms of area, intensity, and frequency. The targeted patterns of variability are informed by knowledge of natural disturbance patterns (Fig. 2). By reintroducing the dynamics typical of

natural disturbances, these practices promote the creation of structurally diverse forests, which better maintains natural functional and biological diversity (Attiwill 1994, Hunter 1999, Lindenmayer and Franklin 2002). Additionally, by maintaining a landscape-level cover of forest in various stages of regeneration, NDE ensures a continued diversity of opportunities for multiple uses of the forest landscape (e.g., recreation, berry and mushroom picking, nature tourism, etc.).

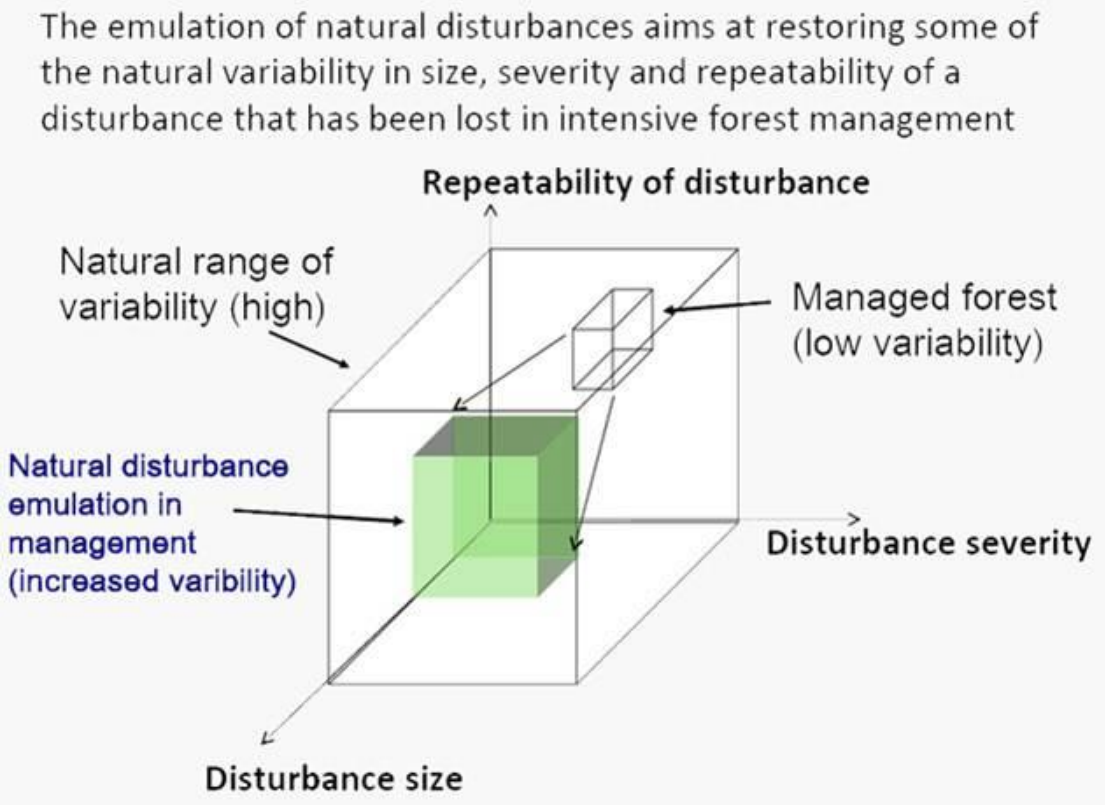


Figure 2. Aim of natural disturbance emulation in forest management (Bergeron et al. 2002)

NDE forestry employs a variety of silvicultural methods to recreate small- to large-scale natural disturbance patterns (Fig. 3). Since small-scale disturbances are typically the most frequent disturbance in the boreal forest, harvesting practices which create a mosaic of small- to medium-scale gaps are considered an important tool for supporting stand-scale structural variability in these regions (Runkle 1981, Coates and Burton 1997, Angelstam 1998, Perera et al. 2004, Caron et al. 2009, Kneeshaw et al. 2011). Such practices include partial, gap and selection harvesting (Fig. 3).

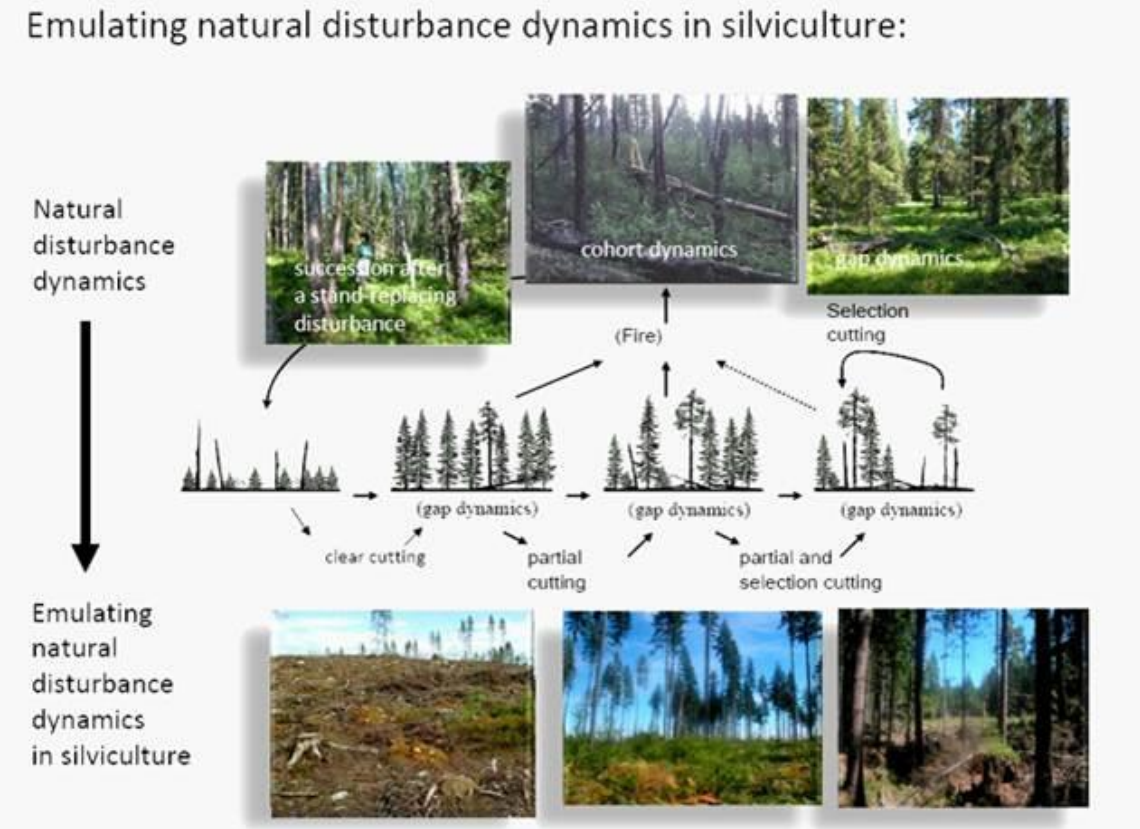


Figure 3. Silvicultural applications of natural disturbance emulation in the boreal forest (Kuuluvainen 2009)

Although the general success of gap-creation in promoting structural diversity has been demonstrated, the processes and dynamics of within-gap regeneration are quite variable and are often misunderstood. In order to implement NDE, forest managers still need access to more reliable information and better tools (e.g., models) to help assess both the short- and long-term implications of NDE and its related management practices.

1.2. Gap-level heterogeneity and effects on natural regeneration

The creation of forest gaps alter the local environmental conditions in ways that tend to promote natural regeneration in spruce dominated boreal forests (Hytteborn et al. 1987, Leemans 1990, Leemans 1991, Liu and Hytteborn 1991, Drobyshev 2001), both for seedlings established before the gap creation (called advance regeneration) and for seedlings which will establish after (Fraver et al. 2008). These altered environmental conditions include new light regimes (Poulson and Platt 1989), new microhabitats (Gray and Spies 1996, Kuuluvainen and Juntunen 1998, McCarthy 2001), new soil moisture conditions (Gálhidy et al. 2006), new soil nutrient profiles (Duchaufour 1982, Kimmins 1987), and new competition dynamics between

seedlings and trees across the newly created gap-level gradients (Goldberg 1990, Kuuluvainen et al. 1993, Palik et al. 1997). The various gap-level ecological factors which affect the patterns of seedling and vegetation regeneration have been summarized by Malcolm et al. (2001), and are shown in Figure 4 below.

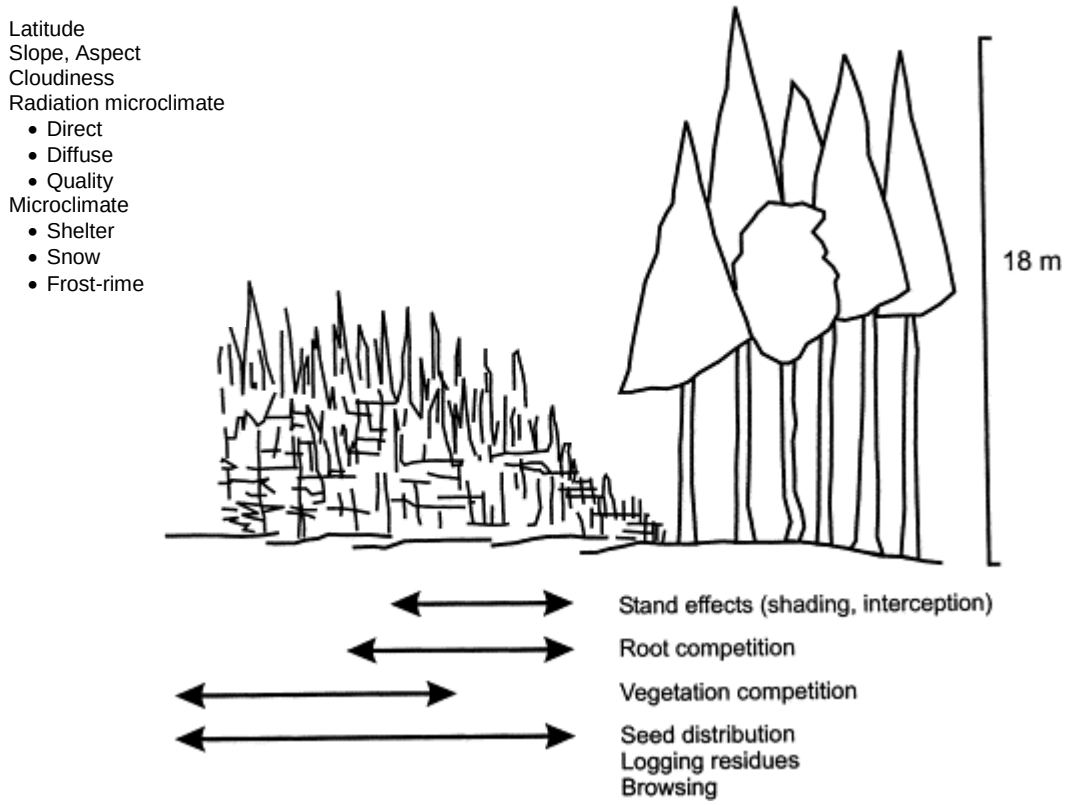


Figure 4. Ecological factors affecting natural regeneration across an average forest gap (Malcolm et al. 2001)

The processes and dynamics of natural regeneration are complex and often quite variable both spatially and temporally. The patterns of natural regeneration are determined by compounding effects of various forest, site and harvesting characteristics over time. Research has shown that after forest harvesting, the recruitment, survival and growth of tree seedlings vary primarily as a function of climatic factors, seed crops, gap size, above- and below-ground competition with other seedlings and trees, vegetation, microsite and topographic conditions, position in the gap (including both distance from gap edge and cardinal position), and time since gap creation (Pukkala and Kolström 1992, Clarke 1992, Kuuluvainen 1994, Örlander and Karlsson 2000, Hanssen 2002, Hanssen 2003, Hanssen et al. 2003, Valkonen and Maguire 2005, Valkonen et al. 2011).

The effects of each of these factors on regeneration have largely been researched individually, or in conjunction with a small number of other factors. Sections 1.2.1 to 1.2.3 provide an overview of the existing literature on the relationships between gap characteristics and the patterns of natural regeneration of Norway spruce (*Picea abies* (L.) Karst.) and birch species (*Betula pendula* Roth., *Betula pubescens* Ehrh.). Only factors included in this study's measurements will be discussed, namely position within the gap and residual forest, microsite types, and topography. This specific set of factors was chosen because, according to the literature, they most significantly affect the spatial patterns of vegetation and seedling regeneration across gaps. Furthermore, these factors are relatively simple to measure and complement each other quite well for data analyses purposes. Where possible, the effects of these factors on germinants (seedlings of only a few years of age) are discussed separately.

1.2.1. Position in the gap

Within the gap environment there exist important spatial gradients in light availability, temperature (soil and air), soil moisture and nutrient availability (Dai 1996, Huggard and Vyse 2002b). These environmental conditions greatly influence the patterns of seedling and vegetation regeneration across the gap, a phenomenon which is sometimes referred to as gap partitioning (Wayne and Bazzaz 1993a, Wayne and Bazzaz 1993b, Bazzaz and Wayne 1994, Sipe and Bazzaz 1995, Gray and Spies 1996).

The gap edge zone has the greatest range of microclimatic and competition dynamics, and consequently has received much attention in research on vegetation and seedling growth (Chen et al. 1993, Matlack 1993, Chen et al. 1995, Cadenasso et al. 1997, Matlack and Litvaitis 1999, Huggard and Vyse 2002a, Huggard and Vyse 2002b). Small- to medium-sized gaps are found to express the most variable ecological responses to gap creation because of their large ratio of edge to gap interior (Coates 2000, Diaci and Boncina 2005, Friesen and Michaels 2010, Mallik et al. 2013, Kern et al. 2014). Small gaps often mimic the environmental conditions of closed-canopy forests, and larger gaps tend to present similar environmental conditions to clear-cuts (Coates 2000, Huggard and Vyse 2002b, Diaci and Boncina 2005, Friesen and Michaels 2010, Mallik et al. 2013). The region of influence can extend to distances of 15m from the forest edge (Biswas and Mallik 2010), and up to 5–10m into the residual forest stand (Stewart and Mallik 2006, Braithwaite and Mallik 2012).

For various forest types, studies have shown that the growth and survival of seedlings is limited by proximity to gap edge (Kuuluvainen and Pukkala 1991, Bradshaw 1992, Hansen et al. 1993, Kuuluvainen 1994, Cadenasso et al. 1997, Burton 2002, Huggard and Vyse 2002a, Huggard and Vyse 2002b, York et al. 2003). This has also been implicitly proven for Norway spruce (De Chantal et al. 2003, Hanssen 2003). One reason which might explain these patterns is an increase in root competition for below-ground resources from trees at the gap edge zone (Kuuluvainen et al. 1993, Caldwell et al. 1995, Nilsson et al. 1996, Örlander et al. 1996, Jäderlund et al. 1997, Brockway and Outcalt 1998). This effect is especially important in Norway spruce-dominated forests because of the strongly horizontal and shallow (depths of up to 20cm) orientation of their root systems (Ammer and Wagner 2002). In gaps within Norway spruce-dominated forests, this effect is strongest within a 5m distance from the surrounding edge trees (Taskinen et al. 2003).

Another factor which explains these patterns of limited growth at the edge zone is the spatial variability in solar radiation across the forest-gap gradient. Solar radiation affects vegetation and seedling growth directly through its important role in photosynthesis, and indirectly through its impacts on soil and air temperatures, soil moisture content and on seasonal patterns of snowmelt, among others (Huggard and Vyse 2002b, Schumann et al. 2003). In general, sunlight and temperature (air and soil) are considered of primary importance in explaining the growth patterns of seedlings and vegetation (Chazdon and Fetcher 1984, Nakashizuka 1985, Canham 1988, Raich and Gong 1990, Dai 1996). Although the exact regimes of solar radiation are a function of latitude and the height of the residual forest canopy, studies showed that for gaps smaller than 60m in diameter the average amount of radiation which reaches the ground surface at different positions inside the gap can range from approximately 20–60% of the total incident radiation (Dai 1996, De Chantal et al. 2003). Huggard and Vyse (2002b) showed that maximum radiation levels were reached within one measure of the average tree length away from the edge towards the gap center. Additionally, Canham et al. (1990) found that for gaps with areas of up to 1000m^2 (diameters of up to ~30m), the daily duration of direct radiation at the ground surface was usually less than four hours. In other words, gaps smaller than ~30m in diameter receive only 50% of full incoming radiation; diameters need to exceed ~50m before gaps can receive over 75% of full incoming radiation (Coates and Burton 1997).

As a consequence of the solar geometry in higher latitudes, the patterns of solar radiation also vary according to the cardinal position in the gap (N, S, E, or W), with the greatest levels of radiation occurring at the northern-central gap positions (Canham et al. 1990). This effect also extends into the residual forest stand, where radiation levels can be as high as 50% of incoming levels inside the forest edge in the northern gap edge (De Chantal et al. 2003), compared to average levels of 8% for all edge positions combined (Dai 1996). This affects the patterns of seedling emergence and growth. For example, several studies found increased growth rates for spruce seedlings (Dai 1996, Huggard and Vyse 2002b, Diaci and Boncina 2005) and greater numbers of birch seedlings (Liu and Hytteborn 1991, Prévost et al. 2010) in the northern positions of the gap. This shift in composition towards the northern gap regions has also been observed for understory vegetation (Fahey and Puettmann 2008, Friesen and Michaels 2010). Regardless of the effects of solar geometry, most studies conclude that gap centers tend to promote a greater productivity and a greater diversity in tree and vegetation species than the surrounding forest matrix (Dai 1996, Schumann et al. 2003, Valkonen et al. 2011, Mallik et al. 2013). However, there still exists a great deal of variability in the patterns of regeneration within the inner gap, particularly between tree species.

Because of the shade-intolerant nature of birch species (Perala and Alm 1990a, Ren et al. 2015), they are greatly affected by the variable patterns of solar radiation across the gap environment. Consequently, birch seedlings grow more slowly and tend to be less numerous in shaded edge and residual forest stand environments, and generally increase in productivity away from the edge towards the gap center (Dai 1996, Valkonen et al. 2011). However, in small gaps (diameters of less than about 10m), the low light levels limit the regeneration of birch seedlings (Runkle and Yetter 1987, Liu and Hytteborn 1991, Busing 1994, Battles and Fahey 2000, Huth and Wagner 2006). Other authors noted that in small gaps, the effects of proximity to the gap edge can be negligible because of the overall low levels of light inside the gap (Hughes and Bechtel 1997, York et al. 2003, Friesen and Michaels 2010). In larger gaps (diameters greater than about 30m), Huth and Wagner (2006) found very few birch seedlings in the gap interior, which was explained by the dense cover of grasses. Similarly, Friesen and Michaels (2010) found that for many species, seedling height increased with increasing gap size, but only up to areas of areas of around 1000m^2 (diameters greater than about 30m); from 1000–5000m^2, gap size had little influence on seedling height because of the more uniform levels of incoming radiation. Therefore, although some patterns exist, the effect of the distance from the edge on birch seedlings seems to also largely depend on

factors such as gap size, competition with vegetation and microsite conditions (Liu and Hytteborn 1991).

Since Norway spruce seedlings are more shade tolerant, they tend to successfully establish and are often even more numerous in smaller gaps (Liu and Hytteborn 1991) and in shaded gap edge environments (Dai 1996, Huggard and Vyse 2002a, Hanssen 2003, Valkonen et al. 2011). Because of lower levels of solar radiation, edge environments experience less soil evaporation and reduced competition compared to the more central gap positions. These factors may promote the establishment of seedlings of shade-tolerant species. However, Dai (1996) showed that although Norway spruce established in a greater range of light levels, to reach their maximum annual growth they required higher levels of light (the same level as for the birch species). Liu and Hytteborn (1991) confirmed these findings, showing that although Norway spruce seedlings were more numerous in small gaps, they grew taller on average in larger gaps.

Some authors suggest that the distance to seed trees may partly explain the greater numbers of spruce seedlings established in the cleared edge zone (Huggard and Vyse 2002a, Huggard and Vyse 2002b, Hanssen 2003). Since spruce seeds are relatively heavy, they don't typically fall further than one to two average tree lengths from the parent tree (Hesselman 1938, Huggard and Vyse 2002b). Consequently, the number of seedlings which reach the ground normally decreases with increasing distance from the parent tree (forest edge) (Skoklefald 1992a, Hanssen 1996, Galipeau et al. 1997, Asselin et al. 2001). Although distance from seed trees might limit seedling establishment further from the edge, many authors agree that it should not be a significant concern for the success of natural regeneration in small- to medium-sized gaps (diameters of less than around 80m); factors such as microsite conditions may play a larger role in the long-term success of regeneration (Heikinheimo 1932, Heikinheimo 1937, Lehto 1956, Perala and Alm 1990a, Ackzell 1994, Huggard and Vyse 2002b).

1.2.2. Microsites

Forest gaps also exhibit a large range of microsites and microhabitats (Kuuluvainen and Juntunen 1998), all of which are said to play a central role in determining the success of tree seedling establishment and growth (Skvortsova et al. 1983, Beatty 1984, Hytteborn et al.

1987, Hytteborn and Packham 1987, Eriksson and Ehrlén 1992, Zasada et al. 1992, Kuuluvainen et al. 1993, Kuuluvainen 1994, Carlton and Bazzaz 1998, Diaci 2002, Hanssen 2003, Diaci and Boncina 2005). Each microsite type affects seedling regeneration in its own unique way, and the effects often vary among tree species (Grenfell et al. 2011). Here, only the effects of microsites included in the study will be discussed, namely that of stones, logs and stumps (young and decayed), duff (leaves, branches, bark and other organic material, in various stages of early decomposition), slash (fine to coarse woody debris created during harvesting operations), and bare mineral soil or humus.

Two overarching categories of microsites exist, those which were underlying (permanent) and those created through the harvesting operations. Underlying microsites include decayed stumps and logs, and soil/moss-covered stones. Slash, young stumps and logs, and bare mineral soil or humus are some examples of microsites created through harvesting. Some microsites are included in both categories or result from a combination of both, such as duff and bare stones. Unless mechanical scarring and mounding techniques are applied at the site, harvesting operations do not significantly alter topography, which can therefore be considered to be an underlying factor.

For Norway spruce seedlings, the suitability of moss- or soil-covered stones as a substrate has mixed reports. Some studies report that they are favorable substrates for seedling establishment and growth (Hytteborn and Packham 1987, Kupferschmid and Bugmann 2005, Valkonen and Maguire 2005), while others report the contrary (Kathke and Bruelheide 2010b). This discrepancy may be a result of the age of the seedlings at the time of measurement; while covered rocks may be less suitable for the establishment of young seedlings (or germinants), they may nonetheless present lower inter-seedling competition resulting in greater long-term regeneration success (Kuuluvainen and Kalmari 2003, Kathke and Bruelheide 2010b). Covered stones were not often described as suitable substrates for birch seedling regeneration.

Stumps, roots and logs in varying stages of decomposition are often important microsites for seedling regeneration, especially for Norway spruce (Hytteborn and Packham 1987, Liu and Hytteborn 1991, Hofgaard 1993, Kuuluvainen 1994, Kuuluvainen et al. 1998b, Ulanova 2000, Zielonka and Piątek 2004, Kupferschmid and Bugmann 2005, Valkonen and Maguire 2005, Motta et al. 2006, Zielonka 2006, Kathke and Bruelheide 2010b). Decayed logs and

stumps are also important regeneration microsites for birch species (Liu and Hytteborn 1991), and can be especially important for birch seedlings in their early stages of growth (germinants) (Grenfell et al. 2011). Since they are elevated compared to the forest floor, logs or stumps can favor seedling establishment by reducing the amount of competition with vegetation (Sollins et al. 1987, Harmon and Franklin 1989, Kirchner et al. 2011) and limiting the access of slugs and rodents (Jonsson and Hofgaard 2011). Some studies stressed that logs and stumps in advanced stages of decomposition are relatively more important for regeneration than those in earlier stages of decomposition (Kuuluvainen and Kalmari 2003, Zielonka and Piątek 2004, Zielonka 2006, Robert et al. 2012). As logs and stumps decay, their physical and chemical properties change. Wood in later stages of decay tends to have a greater water holding capacity as compared to mineral soil, contains more mycorrhizal fungi that can support seedling growth, and has an increased nitrogen content partly as a result of greater microbial action (Jurgensen et al. 1987, Eissenstat and Newman 1990, Hendrickson 1991, Zimmerman et al. 1995, Zielonka 2006). Therefore, the age of the stumps or logs is a very important consideration in assessing their effects on seedling establishment and growth.

Duff, or litter as it is sometimes called, can have drastically different impacts on seedling regeneration depending on its characteristics, such as its dominant composition or thickness (Nilsson et al. 1999). For example, duff dominated by Norway spruce needles often have negative effects on the germination and growth of spruce and birch seedlings (Kinnaird 1974, Gallet 1994, Huth and Wagner 2006, Ren et al. 2015), due in part to allelopathic effects caused by the decomposing needles (Gallet and Lebreton 1995). Research with other species has shown that very thick duff layers can be detrimental to seedling establishment (Nakamura 1992, Jeglum and Kennington 1993, Groot and Adams 1994), and that seedlings preferentially establish in thinner duff layers (Kinnaird 1974). Conversely, on duff-dominated microsites with mixed compositions, several other studies reported large numbers of Norway spruce seedlings (Hanssen 2002, Hanssen 2003, Hunziker and Brang 2005) and maximum birch species growth (Hartig and Lemke 2002, Huth and Wagner 2006). Therefore, it is especially important to consider the dominant composition and characteristics of the duff in order to assess its impact on seedling regeneration (Nilsson et al. 1999).

Layers of slash (fine to coarse woody debris created during harvesting operations) can be extremely variable in terms of their thickness and density, the size-distribution of the branches and twigs, the content of tree cones or seeds, and the species of their trees of origin.

Consequently, the effects of slash on seedling regeneration are often quite variable and it is difficult to generalize. Slash could negatively affect seedling establishment by forming a barrier and preventing seedlings from reaching the ground. Additionally, slash could significantly reduce the amount of radiation reaching the ground surface and therefore the seedlings that do manage to establish. On the other hand, some studies have reported a positive correlation between Norway spruce densities and the presence of slash (Valkonen and Maguire 2005, Diaci and Boncina 2005). Being shade-tolerant, Norway spruce seedlings may benefit from the microsite conditions of slash since such conditions can cause a reduction in competition from understory vegetation or other tree seedlings (Olsson and Staaf 1995). However, this cooler and shaded environment is likely detrimental to the establishment and growth of light-demanding birch species. This has been confirmed by Karlsson et al. (2002), who found that the removal of slash after harvesting had a significant positive effect on the establishment of birch seedlings.

Microsites of bare mineral soil or bare humus can be created either intentionally (by mechanical site preparation techniques) or unintentionally during mechanical harvesting operations. Additionally, they can be created naturally through disturbance events such as windthrows, where uplifted roots leave behind a scarified ground surface. The ground surface in forests dominated by Norway spruce typically consists of thick layers of moss and/or humus, conditions which are typically understood as an inhibitory factor to seedling establishment (Sirén 1955). Therefore, by removing these surface layers and creating a more hospitable microsite, these disturbance processes can facilitate spruce and birch regeneration (Hagner 1962, Yli-Vakkuri 1963, Kinnaird 1974, Liu and Hytteborn 1991, Karlsson and Örlander 2000, Karlsson 2001, Karlsson et al. 2002, Nilsson et al. 2002, Diaci and Boncina 2005, Grenfell et al. 2011, Jonsson and Hofgaard 2011). This type of microsite is especially important for seedlings in early growth phases (germinant) (Yli-Vakkuri 1963, Valkonen and Maguire 2005).

1.2.3. Topography

Irrespective of its origin or its surface layer characteristics, topography can affect microsite conditions, particularly with respect to hydrology. Since vegetation and seedlings are greatly influenced by the availability of moisture, topography can in turn influence the growth and competition dynamics at the microsite scale. For Norway spruce, low moisture levels can

significantly impede germination and the subsequent establishment of seedlings (Bjor 1971, Skoklefald 1992b). This could occur on sloped and particularly mounded (convex) topographies, which tend to facilitate drainage and reduce water infiltration (by increasing the amount of surface runoff) during precipitation events. In combination with the erosion of soil particles from gravity, these hydrological agents also render the soil environment on mounds and slopes more unstable and thus more unfavorable for seedling establishment.

A combination of these factors could explain why studies have shown that mounds support lower numbers of both birch and Norway spruce seedlings (Ilisson et al. 2007, Vodde et al. 2010). Still, mounds can also host diminished levels of competition with vegetation while simultaneously providing a greater access to light, and sometimes supporting higher levels of nutrients (Gastaldello et al. 2007). Consequently, mounds also reportedly favor the regeneration of Norway spruce and birch seedlings (Liu and Hytteborn 1991, Kuuluvainen and Juntunen 1998, Ulanova 2000, Kuuluvainen and Kalmari 2003, Diaci and Boncina 2005, Gastaldello et al. 2007, Vodde et al. 2015). The environmental conditions of mounds are especially relevant for the success of light-demanding species, if they can initially succeed at establishing in these locations. Accordingly, Carlton and Bazzaz (1998) observed higher growth rates for birch seedlings established on mounded topographies. Slopes, on the other hand, could favor seedling regeneration where soil water contents may be greater. Such sites would include those with low levels of incoming solar radiation, with cool climates or with particularly high clay contents in the soil. For example, Diaci and Boncina (2005) observed more successful regeneration of Norway spruce on slopes (vs. mounds or depressions) in small forest gaps in subalpine forests—sites which have a relatively cool climate and lower levels of solar radiation because of shading from the surrounding trees.

Seedlings preferentially accumulate in pitted topographies, whether transported through gravity (for larger seeds, e.g. spruce cones), or washed in by water movement or wind (for smaller and lighter birch seeds or individual spruce seeds). Furthermore, water, also carrying other nutrients in solution, would also accumulate in depressions and thus encourage plant and seedling growth. Accordingly, depressions on sites dominated by mineral soils tend to promote the establishment of greater numbers of birch and Norway spruce seedlings (Kuuluvainen and Juntunen 1998, Hanssen 2003, Kuuluvainen and Kalmari 2003, Diaci and Boncina 2005, Ilisson et al. 2007, Vodde et al. 2010, Vodde et al. 2015). However, the long-term growth and survival of seedlings is also sometimes limited in depressions, possibly a

consequence of increased competition and/or self-thinning between seedlings, or because of greater mortality resulting from inundation (Hanssen 2003, Ilisson et al. 2007). Vodde et al. (2010) also observed that both Norway spruce and birch seedlings preferred shallow rather than deep topographic depressions, perhaps because of less severe flooding levels.

1.3. Understory vegetation

1.3.1. Relationship with seedling regeneration

As a result of its significant competition for resources such as light, water and nutrients, understory vegetation plays an important role in the success of early seedling regeneration (Sirén 1955, Hytteborn et al. 1987, Kuuluvainen 1994, Örlander et al. 1996, Hornberg et al. 1997, Jäderlund et al. 1997, Schrötter 1998, Cornett et al. 1998, Nilsson and Wardle 2005). In many cases, the presence of vegetation tends to have a negative impact on the regeneration success of seedlings (Davis et al. 1999, Lof 2000, King 2003, Coll et al. 2004, Hytönen and Jylhä 2005). Generally, it is the vegetation growing closest to the seed/seedling which has the most significant impact on its establishment and growth (Hanssen 2003). Also, Hytönen and Jylhä (2005) noted that the belowground competition for water and nutrients from vegetation can be more significant than the aboveground competition for light. However, the exact nature of these effects varies by species as a result of morphological differences of both the seedlings and the understory vegetation (Goldberg 1990).

The interactions between seedling regeneration and grasses or sedges have received a lot of attention in the literature. After gap creation, grasses/sedges are often one of the first types of vegetation to colonize the gap interior, especially in medium- to large-sized gaps (diameters >25m) (Whitmore 1978, Leder 1992, Yamamoto 2000, Hartig and Lemke 2002, Holeksa 2003). Grasses quickly develop dense root mats at the same depth as seedling roots, making them important competitors for water and nutrients (Moser 1965, Robic 1985, Fanta and Kobus 1995, Betz 1998, Hanssen 2003, Picon-Cochard et al. 2006). Grasses can grow to be fairly tall, making them also strong competitors for light (Huston and Smith 1987, Veer and Kooijman 1997, Harper and Macdonald 2002), causing a reduction of light levels of up to 77% at the ground level (Picon-Cochard et al. 2006). For these reasons, sites occupied by grasses are typically linked to low seedling densities for both Norway spruce (Hertz 1932, Yli-Vakkuri 1963, Hanssen 2002, Hanssen 2003, Pages and Michalet 2003, Diaci and

Boncina 2005, Kupferschmid and Bugmann 2005, Valkonen and Maguire 2005, Valkonen et al. 2011) and birch species (Hartig and Lemke 2002, Huth and Wagner 2006). However, Huth and Wagner (2006) found that the few birch seedlings which successfully established in grasses tended to grow better over time, likely because of the greater light levels which characterize areas dominated by grasses.

After gap creation, shrubs and dwarf shrubs are also able to rapidly colonize the gap interior (Harper and Macdonald 2002, Holeksa 2003, Gastaldello 2005). As a result of above-ground competition for light and below-ground competition for resources (Jäderlund et al. 1997), shrubs and dwarf shrubs generally limit the establishment and growth of Norway spruce and birch seedlings (Hertz 1932, Gimingham 1984, Skoklefald 1992b, Hanssen 2002, Hanssen 2003, Diaci and Boncina 2005, Valkonen and Maguire 2005, Kupferschmid and Bugmann 2005, Prévost et al. 2010). In addition, dwarf shrub species of the Ericaceae family (e.g., *Vaccinium myrtillus, V. vitis-idaea,* and *Empetrum nigrum*) can hinder seedling regeneration through allelopathic mechanisms (Zackrisson and Nilsson 1992, Pellissier 1993, Nilsson et al. 1993, Gallet 1994, Gallet and Lebreton 1995, Jäderlund et al. 1996, Nilsson et al. 1999). Furthermore, the roots of ericaceous shrubs can have mycorrhizal hyphae which are capable of rapidly removing nutrients from the soil, effectively reducing the nutrient supply available to seedlings (Zackrisson et al. 1997).

At moister sites, ferns can also rapidly dominate the understory vegetation component of regeneration after harvesting (Holeksa 2003, Man et al. 2009). Ferns are extremely effective at competing with seedlings for light (both in full sunlight and in shaded conditions), given their rapid growth of tall and often large fronds (den Ouden 2000, Dumas 2002, Harper and Macdonald 2002, Coomes et al. 2005, Marrs and Watt 2006). Some studies have shown that ferns are so effective at competing that, at the site-level, they can even completely inhibit the regeneration of certain species (Humphrey and Swaine 1997, Russell et al. 1998). Indeed, studies have shown that sites dominated with ferns tend to have limited Norway spruce and birch seedling regeneration (George and Bazzaz 1999a, George and Bazzaz 1999b, Kupferschmid and Bugmann 2005). George and Bazzaz (1999a) discovered that ferns also limit the initial establishment of birch seedlings by hindering the exposure of their seeds (small and light) to the soil or ground surface. Since the seeds (and cones) of Norway spruce are relatively large and heavy, their establishment is generally less impaired by the presence of ferns (Dolling 1996).

To various extents, the removal of the overstory canopy through forest harvesting also promotes the growth of herbaceous vegetation species (Kooijman et al. 2000, Man et al. 2009, Valkonen et al. 2011). Herb species can also be extremely competitive in terms of light resources given their rapid growth of often large leaves. Some studies showed that, like ferns, they are able to 'filter' the types of species which can successfully regenerate in their vicinity (Takahashi 1997, George and Bazzaz 2003, Lawes and Chapman 2006, Itô and Hino 2007). Bell et al. (2000) reported that of all early successional species which colonize after harvesting in boreal forests, herbs were on average ~30% more effective at competing for resources as compared to regenerating seedlings. Furthermore, studies have found that extensive coverage of herbs hinders spruce and birch seedling regeneration (Gimingham 1984, Bell et al. 2000, Valkonen and Maguire 2005). However, Valkonen and Maguire (2005) found that the presence of herbs was linked to regions of greater seedling density, likely because herbs compete with grasses and mosses, which can even more severely impede seedling establishment.

In the boreal region, mosses tend to dominate the vegetation portion of the forest floor (Kuuluvainen 2002). As discussed, after the harvest of trees the forest floor is exposed to an increased amount of light, triggering a subsequent rise in the level of competition from colonizing vegetation. This rise in competition can significantly reduce the cover of mosses, especially with increasing distances from the residual forest edge (Man et al. 2008, Valkonen et al. 2011). Nevertheless, some cover of mosses still persists after gap creation, especially in the shadier gap edge zones or in the interior regions of smaller gaps, where environmental conditions remain closer to those of the closed-canopy forest (Huth and Wagner 2006). Studies on the suitability of mosses as substrates for the establishment of seedlings have reported mixed findings. Some studies reported that moss-dominated substrates favored the establishment of seedlings of Norway spruce and birch species, among others (Moser 1965, Liu and Hytteborn 1991, Leder 1992, Lässig et al. 1995, Coates and Burton 1997, Malcolm et al. 2001, Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Huth and Wagner 2006), whereas others reported the contrary (Hertz 1932, Yli-Vakkuri 1963, Kinnaird 1974, Steijlen et al. 1995, Hanssen 2002, Hanssen 2003, Valkonen and Maguire 2005). The suitability of mosses as a substrate for seedling establishment and growth appears to be related to the thickness of the moss layer and its ability to hold moisture. Thinner moss layers are found to be more suitable for seedling establishment and to have lower rates of mortality compared to thicker mosses of the same composition (Kinnaird 1974, Brang 1996, Iijima and

Shibuya 2010). However, since moisture availability also plays an important role in determining the effects of moss layer thickness, the local climatic conditions should also be considered.

The species of the mosses also appears to have a significant influence on the suitability of the moss layer. For example, mosses of the *Sphagnum* genus are often reported as being favorable for Norway spruce and birch (and other) seedling establishment (Kinnaird 1974, Ohlson and Zackrisson 1992, Jeglum and Kennington 1993, Fleming and Mossa 1994, Hornberg et al. 1997, Hanssen 2002, Hanssen 2003, Kupferschmid and Bugmann 2005). This may be because *Sphagnum* species are effective at capturing and retaining moisture, both from the atmosphere and from their immediate surroundings (Du Rietz et al. 1952). However, due to their rapid growth rates (Pakarinen and Rinne 1979), some *Sphagnum* species are also capable of overgrowing small seedlings, causing increased seedling mortality in the long-run (Groot and Adams 1994, Ohlson 1995, Hanssen 2003). To a lesser extent, mosses of the *Polytrichum* genus have also been reported as more favorable substrates for the establishment of Norway spruce seedlings, likely largely due to their moisture-holding capabilities (Hanssen 2003, Kupferschmid and Bugmann 2005).

Feather mosses (e.g., *Hyloconium splendens* and *Pleurozium shreberi*) and those of the *Dicranum* genus are often described as especially poor substrates for the establishment of Norway spruce, birch and pine seedlings (Steijlen et al. 1995, Hanssen 2003, Valkonen and Maguire 2005). Research shows that feather mosses (among other boreal forest mosses) are capable of quickly and effectively absorbing nutrients from their environment, often at the expense of seedlings and other vegetation (Oechel and Van Cleve 1986, Zackrisson et al. 1999). Furthermore, since the litter produced by dead feather mosses decays very slowly, it often forms thick mats below the living moss layer, and releases nitrogen at a slower rate than other litter (Wardle et al. 2003). These factors combined could render the feather moss substrates fairly nutrient poor, thus impeding the establishment and survival of seedlings. Mosses of the *Dicranum* genus, on the other hand, are reportedly even poorer seedbeds than feather mosses (Hanssen 2003). This has been explained in part by the fact that these species tend to colonize very dry substrates (rocks or shallow soil), which could pose a moisture limitation for seedlings germinating or growing amongst them (Hanssen 2003).

Fewer studies have been carried out on the relationship between lichens and seedling regeneration. Some studies on Scots pine regeneration show that lichens of the *Cladina* genus (reindeer lichens) may support seedling growth (Steijlen et al. 1995, Zackrisson et al. 1995). Conversely, some studies on birch and spruce species found that the removal of these lichens by reindeer browsing and/or trampling resulted in a greater number of seedlings successfully establishing (Tømmervik et al. 2004, Tømmervik et al. 2005, Tremblay and Boudreau 2011). The effects of lichen on regeneration therefore appear to vary considerably depending on the species of the seedlings and the thickness of the lichen layer.

In summary, although some vegetation-dominated substrates can support the regeneration of seedlings, most studies suggest that a dense or continuous cover of most vegetation types is a significantly limiting factor for seedling establishment and growth (Diaci and Boncina 2005, Valkonen and Maguire 2005, Hytönen and Jylhä 2005). Therefore, after gap creation, the spatial and temporal patterns of vegetation growth are to a large extent often capable of determining the success of seedling regeneration across the gap.

1.3.2. Vegetation analysis as a tool

Understory vegetation is able to respond quite rapidly (in as little as ~5 years) to the new microsite and light conditions created by the removal of overstory trees (Harper et al. 2004, Harper et al. 2005, Hill et al. 2005, Stewart and Mallik 2006, Mallik et al. 2013). Species which increase in growth include shrubs grasses or sedges, and early successional light-demanding herb species (Grushecky and Ann Fajvan 1999, Domke et al. 2007). For species of the Ericaceae family, such as *Vaccinium* spp., this rapid growth response is related to their ability to adapt their physiology and morphology in order to take advantage of the increased light availability (Mallik 1994, Mallik et al. 2012). Several studies have shown that understory vegetation is one of the most important factors controlling the patterns of natural regeneration of seedlings (Schrötter 1998, Diaci and Boncina 2005). Through allelopathic mechanisms, some species of vegetation can also directly inhibit or limit seedling establishment and growth (Nilsson and Zackrisson 1992, Pellissier 1993, Dolling et al. 1994, Gallet 1994, Jäderlund et al. 1998, Mallik and Pellissier 2000). As summarized in Section 1.3.1, vegetation growth after harvest can significantly affect the patterns of seedling regeneration, and is particularly important during the early phases of seedling establishment. Therefore, by analyzing the early patterns of gap-level vegetation regeneration across gaps

we can also better anticipate the success of natural seedling regeneration across the gap environment.

As a whole, understory vegetation is also very sensitive to variations in microsite conditions, topography and resource availability, and their patterns of regeneration reflect this (Palmer and Dixon 1990, Tonteri 1994, Bratton 1994, Gilliam and Roberts 2003, Moffatt and McLachlan 2004, Halpern et al. 2005, Flinn and Vellend 2005). Additionally, the species composition of understory vegetation is fairly diverse, and displays quite variable spatio-temporal patterns of regeneration depending on their physiological capabilities and limitations. Consequently, an analysis of understory vegetation regeneration can be an important tool for revealing the finer-scale nuances of gap-level heterogeneity, and can also help to better understand the processes affecting seedling regeneration across gaps.

2. THE RESEARCH PROJECT DEFINED

2.1. Overview

In North America, the parameters and success of the natural disturbance emulation (NDE) forest management approach have been widely researched (Franklin et al. 1997; Gauthier et al. 2009; Peterson & Anderson 2009; Lindenmayer et al. 2012), but in northern Europe significantly fewer studies have been made on the topic (Gustafsson et al. 2012). Due to a growing interest from scientists, forest owners and the general public, in 2009 the first research and development project on the subject was initiated in Finland. The project is led by the Natural Resources Institute Finland, Luke (formerly the Finnish Forest Research Institute, Metla), and is entitled *Forest management inspired by natural disturbance dynamics* (DISTDYN).

The general aim of DISTDYN is to create a framework through which the effects of various harvesting and management practices aimed at emulating the dominant natural disturbance patterns in boreal Fennoscandian (e.g., Angelstam & Kuuluvainen 2004; Kuuluvainen & Aakala 2011) can be studied on a long-term basis. This project is unique in that it will be implemented on a larger landscape scale, whereas most other research projects in Europe have focused on smaller scales, such as that of a forest stand. Research under the umbrella of the DISTDYN project will include the patterns of post-harvest natural regeneration, the response of various biota, the costs of harvesting using different methods, and the effects on local socio-cultural values, among others. The results of this long-term study will assist in establishing future guidelines and practices aimed at restoring stand dynamics and characteristics which favor the health of habitats in the boreal forest while ensuring the future success of the timber industry and other key socio-economic and socio-cultural values.

Two research areas have already been established under the project. The first was established in 2009 in central Finland, the Isojärvi research area near Kuhmoinen; the second was established in 2010 in east-central Finland, the Ruunaa research area near Lieksa. The first harvests were conducted during the winter of 2009/2010 in Isojärvi, and in 2010/2011 in Ruunaa. This particular study focused on the Isojärvi research area, which is described in more detail in the following sections.

2.2. Disturbance levels and intensities at Isojärvi

The Isojärvi research forest is divided into six treatment blocks of 100–200ha (Fig. 5), within which different harvesting approaches are applied in varying proportions in order to achieve the desired spatial heterogeneity. As a whole, the landscape is characterized by two levels of management intensities: 50% and 90%. The management intensities define the percentage of timber yield to be harvested throughout the rotation period (circa 100 years). The remaining 10 % or 50 % of the forest volume is designated to permanent retention. Within these two management intensities, three different levels of spatial disturbance are applied: small-, intermediate- and large-scale disturbances. Each of the six treatment blocks represents a unique combination of the two possible management intensities and the three possible disturbance levels (Fig. 5).

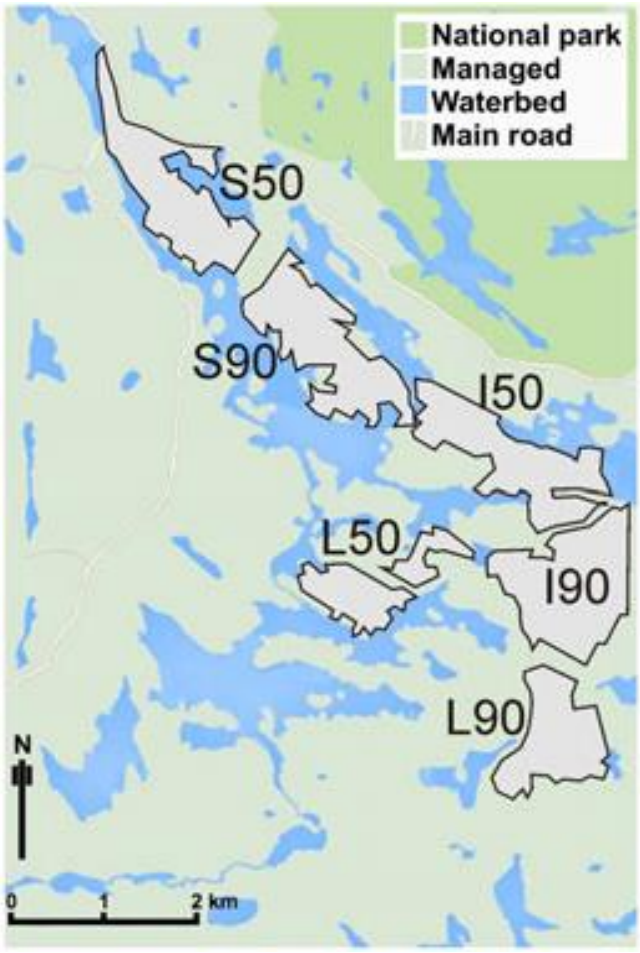


Figure 5. DISTDYN treatment block distribution at Isojärvi. Blocks represents unique combinations of disturbance levels (S = Small-scale, I = Intermediate-scale, L = Large-scale) and management intensities (50% or 90%). (Koivula et al. 2014)

2.3. Harvesting approaches at Isojärvi

In order to emulate natural disturbance patterns and to achieve the varying levels of disturbances and management intensities, four different harvesting approaches are applied: single-tree-selection felling (or simply selection felling), gap felling, partial felling, and clear felling (Fig. 6). Selection felling involves the removal of individual large trees or small groups of trees. Gap and partial felling involve harvesting small irregular patches with areas of ca. 0.1–0.5ha, and diameters of approximately 10–40m and 40–60m, respectively. Clear felling involves the complete harvest of stands 0.5–5.0ha in area, with cutting and regeneration methods appropriate for the site and stand conditions. Additionally, to further increase structural diversity and to ensure the proper density of trees for adequate quality growth, all the forest stands are thinned at some point during their regeneration process. The forest stands are thinned before harvesting (first commercial thinning) and/or after harvesting (thinning of the residual stand).

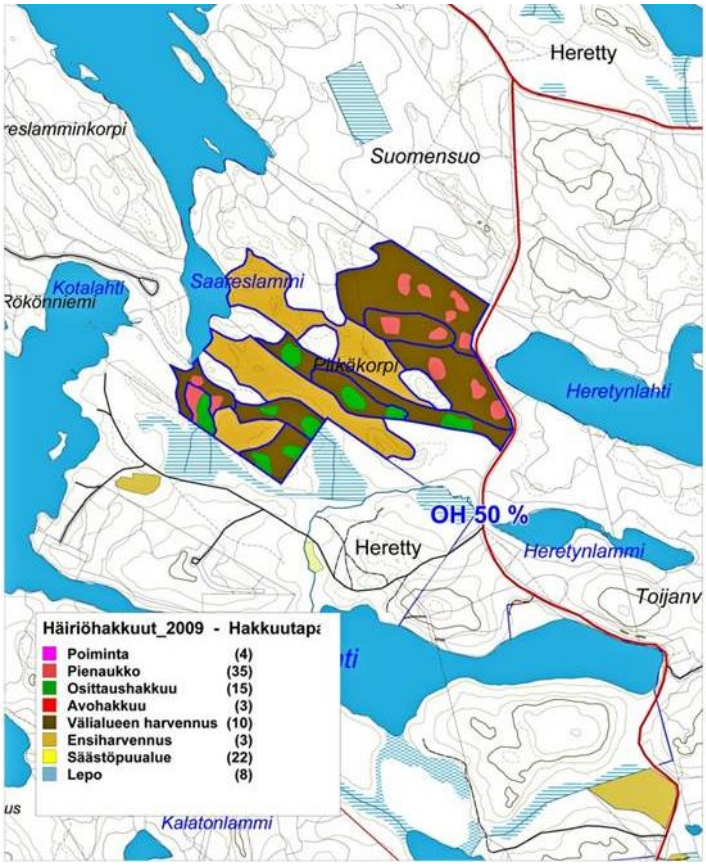


Figure 6. Harvesting in Isojärvi 50% intermediate-scale disturbance block (here referred to as OH50% using Finnish terminology). Gaps are shown in red, and partial harvests in green; the light brown areas represent first commercial thinning, and the dark brown represents thinning in the residual stand. (Metsähallitus)

Various combinations of these forest harvesting approaches are applied on each treatment block in order to emulate the patterns typical of natural disturbance patterns. In the small-scale disturbance level blocks, 75% of the forest harvesting is executed by gap felling and 25% by selection felling. These less severe treatments aim to emulate disturbance patterns caused by storms or insect damage, among others. In the intermediate-scale disturbance level blocks, 75% of the forest harvesting is executed by partial felling and 25% by gap felling. These moderately severe treatments aim to emulate disturbance patterns caused by surface fires or insect outbreaks, among others. In the large-scale disturbance level blocks, 75% of the forest harvesting is executed by clear felling and 25% by partial felling. These fairly severe treatments aim to emulate disturbance patterns caused by wildfires, or other disturbances that kill almost all the trees within a forest stand.

With all harvesting approaches, individual trees or groups of trees (often called 'retention trees') are left uncut within the treatment areas to add structural diversity. The number of retention trees varied as a function of management intensity, from 5–20%. In addition, during each harvest a few high stumps (2–3m tall) were created in order to provide resources and habitat for deadwood-dependent species. The tops of trees and/or branches are also sometimes left at the site. In the context of gaps, 2.5–15% of the trees are left as live retention trees, and 2.5–5% of them are turned into high stumps (examples in Fig. 7).

Figure 7. Retention trees and high stumps inside gap at Isojärvi. *Photo credit:* Margot Downey

As mentioned earlier, this study focused on the Isojärvi research area in Central Finland. It included only the treatment blocks managed for small- and intermediate-scale disturbances. Within these treatment blocks, the early post-harvest natural regeneration patterns of seedlings and vegetation were assessed across suitable forest gaps, including a small zone into their surrounding forest matrix. The gaps included in the study had all been created through the harvesting methods of gap and partial felling. Additionally, in order to obtain the longest post-harvest regeneration period possible, this study focused only on gaps created during the first harvesting treatments (during the winters of 2010 and 2011).

2.4. Objectives and hypotheses

The objectives of this study were to: 1) study the patterns of natural vegetation and tree seedling regeneration (for Norway spruce and birch spp.) five years post-harvest across forest gaps at Isojärvi, and 2) with the help of models, to describe the relationships between the patterns of early seedling and vegetation regeneration, and gap characteristics (distance from gap edge, cardinal position in the gap, and microsite type). Moreover, this study aimed to produce the first vegetation-based dataset for the DISTDYN project, which would later contribute to the analysis of long-term regeneration patterns across the forest gaps at Isojärvi.

Based on results of previous research, the hypothesis is that the most influential gap characteristic is the distance from gap edge. Gap centers would likely promote rapid growth of shade-intolerant species (broadleaf trees, grasses, shrubs and herbs), creating a highly competitive environment; gap edges would likely support greater yields of shade-tolerant species (Norway spruce, mosses, dwarf shrubs) with less competition from understory vegetation. Given the patterns of solar radiation in northern latitudes, a northward skew of both productivity and competition of shade intolerant species is expected, the effect even extending into the residual forest.

The greatest density of birch and Norway spruce seedlings is expected to be found on or near logs and stumps, especially those in more advanced stages of decomposition. Furthermore, bare humus or mineral soil microsites would likely host larger numbers of seedlings as well, but they may already be rare inside the gaps 5 years after harvests. Moss-covered stones may also host a relatively higher number of seedlings, especially of Norway spruce. Microsites

with large covers of duff will likely have fewer seedlings; however, in smaller amounts duff might improve the suitability of the microsite for seedling regeneration. Since both moss-covered stones and duff-dominated microsites are likely unfavorable for the establishment of young seedlings, fewer germinants and a greater proportion of older seedlings would be expected on these sites. Microsites dominated by slash are expected to support greater numbers of Norway spruce seedlings compared to birch seedlings. However the relationship between varying covers of slash and the number of seedlings may be somewhat inconsistent as a result of varying slash thicknesses and compositions.

Depressions will likely promote seedling establishment and growth, whereas mounds or slopes may be limiting. However, over the long term, depressions may become less suitable because of increased levels of competition or inundation, whereas mounds may offer lower levels of both. Consequently, although depressions may show greater overall numbers of both Norway spruce and birch seedlings, it is expected that mounded topographies may have a positive effect on the numbers of older seedlings.

As a result of strong competition for light and nutrients, areas dominated by grasses, shrubs, dwarf shrubs, ferns, and herbs will likely support low numbers of seedlings. In the case of dwarf shrubs, particularly *Vaccinium myrtillus*, allelopathic effects would also contribute to a lower number of established seedlings. The effect of mosses and lichens is uncertain since they vary depending on the layer thickness and the species of both the mosses/lichens and the seedlings. However, areas with large covers of mosses or lichens are likely unsuitable substrates for the establishment of Norway spruce and birch seedlings.

3. MATERIALS AND METHODOLOGY

3.1. Study area

This research was carried out in the DISTDYN large-scale (689ha) experimental forest area in the region of Central Finland (Fig. 8). The experimental forest is situated adjacent to Isojärvi Environmentally Valuable Forest, between the cities of Jämsä (to the North) and Kuhmoinen (to the South). The area is owned and managed by Metsähallitus, in collaboration with the Natural Resources Institute Finland (Luke; formerly the Finnish Forest Research Institute, Metla).

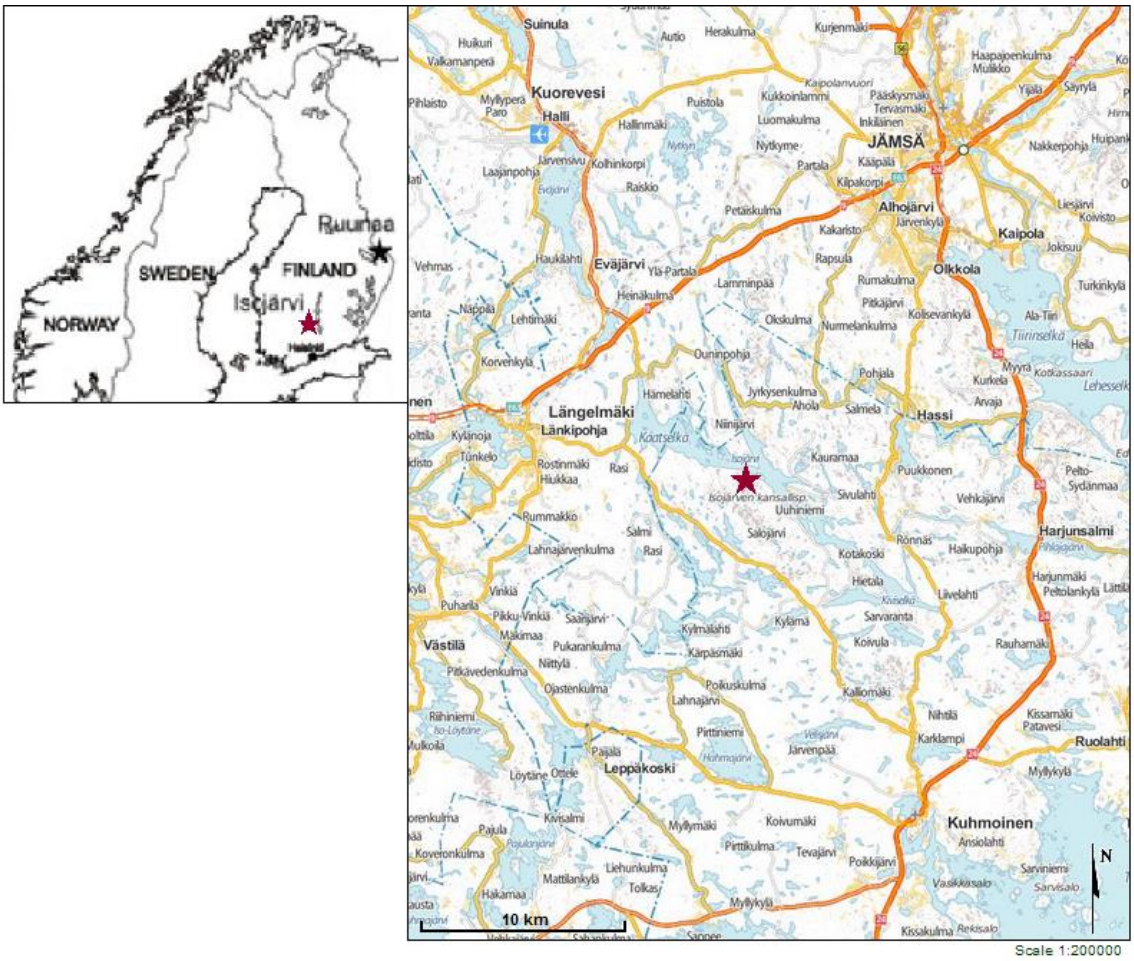


Figure 8. Research area near Isojärvi Environmentally Valuable Forest, Finland (Metsähallitus)

The region experiences a subarctic climate characterized by distinct seasonal variations, ranging from cold snowy winters to warm summers. Based on the 1981–2010 normal period, the mean annual air temperatures are 3–4°C, and mean annual precipitation is of 600–700mm (Pirinen et al., 2012). July is the warmest month, and has an average temperature of about

17°C; the average daily high and low temperatures in July are of 22°C and 11°C, respectively. In general, the growing season is about 5 months long (May–October). The landscape is dominated by forests, small patches of peatland bordering numerous lakes, small creeks and gently undulating topography. The elevation above sea level ranges approximately from 100–150m.

The area is located within the Boreal Forest ecoregion and is generally quite fertile. The forests here are predominantly defined by submesic *Myrtillus* type (58%) and mesic *Oxalis-Myrtillus* type (12%) (as per the site type classification system defined by (Cajander 1909). In this study, fifteen gaps were situated in *Myrtillus* type forest sites and three in *Oxalis-Myrtillus* type forests. The dominant tree species are Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). Mixed species stands also occur, most commonly with silver birch (*Betula pendula* Roth) and pubescent birch (*Betula pubescens* Ehrh.), and occasionally with European aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.), common alder (*Alnus glutinosa* L.) and grey alder (*Alnus incana* Moench). The vegetation is dominated by dwarf shrubs (e.g., *Vaccinium myrtillus*, and *Vaccinium vitis-idaea*), herbs, grasses/sedges, ferns, mosses and lichens.

As with most of Finland's forests, the area has experienced a prolonged history of traditional commercial harvesting. Additionally, most of the peatlands have been drained. However, there had been no regeneration cuttings for over ten years prior to it being officially designated as an experimental forest. Consequently, most of the forest stands are middle-aged; 28% are early-middle-aged and 47% late-middle-aged (Metla, 2013).

3.2. Data collection

3.2.1. Selection of sample gaps

The selection of the gaps for analysis was planned during the months preceding the 2014 field season. The gaps were selected based on the following criteria. The gaps on drained peatland sites or treated with site preparation were excluded. The gaps were selected in the central part of the forest stand to avoid external influences. Sampling areas must not have extended into a neighboring gap. Also, the tree sampling areas were required to remain within the target stand. A maximum of two gaps were chosen for measurement in each forest stand,

in order to ensure a balanced study. All gaps which met these criteria in MT (*Myrtillus* type) or OMT (*Oxalis-Myrtillus* type) forest sites were included in the study. In total, eighteen harvested forest gaps were studied across thirteen distinct forest stands, ranging in size from 0.10–0.36 hectares (mean size of 0.19ha, median size of 0.18ha) (Fig. 9).

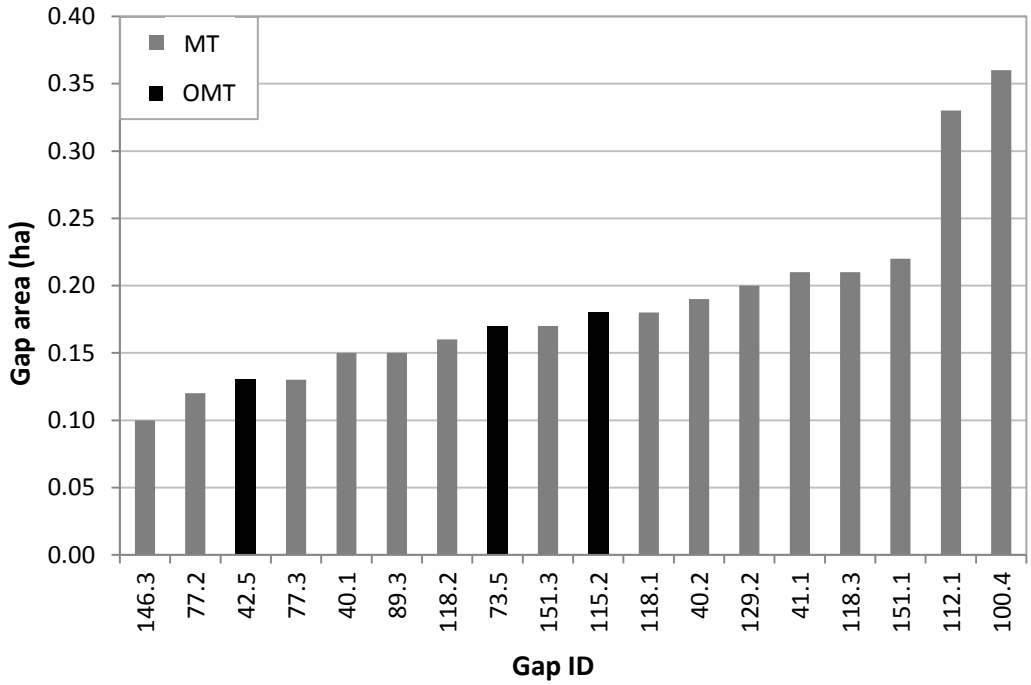


Figure 9. Area and site type of all gaps sampled at Isojärvi. MT = *Myrtillus* Type; OMT = *Oxallis-Myrillus* Type.

Gap sampling design varied as a function of gap size: gaps with diameters <40m were treated as *small gaps*, and those with diameters >40m were treated as *large gaps*. To determine the gap size, two diameter measurements were taken (one for each North-South and East-West orientation) upon arrival at the gap site using a clinometer. Measurements were collected during a 2-month field season starting in August 2014, with continued support from and collaboration with Luke.

3.2.2. Establishing baselines, linear sampling strips and quadrats

Baselines were established in each gap, with East-West and North-South orientations (Fig. 10). In small gaps, one baseline of each orientation was established, each spanning the whole interior of the gap (as is seen in Fig. 10). In large gaps, two baselines of each orientation were established, each extending approximately 20m into the gap interior from the gap edge. As gaps were often uneven shapes, care was taken to ensure each large gap's baselines crossed

the gap's cardinal edges at a central position. In both gap types, each baseline also extended 10m from the gap edge into the remaining forest stand. Gap edge was defined as the point where the baseline crosses the line that connects the bases of the two nearest trees, as per Runkle (1981).

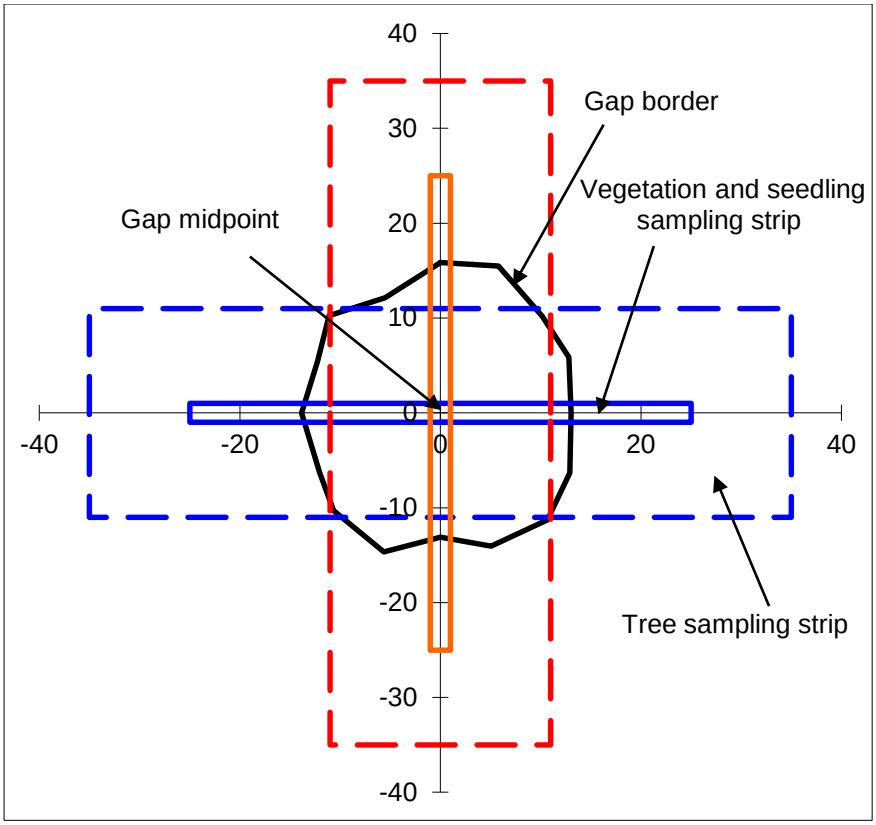


Figure 10. Experimental setup for gap analysis at Isojärvi (Metla/Luke)

In small gaps, baseline 1 was oriented East-West, and baseline 2 North-South. In large gaps, baselines were numbered in a clockwise direction, where strips 1 and 3 were oriented North-South, and 2 and 4 were oriented East-West. For small gaps, the baseline center (coordinates x = 0, y = 0) was at gap midpoint; values increased in each cardinal direction from this point. For large gaps, each baseline was positioned at its own central point along the northern, southern, eastern and western gap edges. Therefore, for large gaps, the baseline centers were located where they crossed the gap edge; values increased in both directions from this point. For both gap sizes, x-values increased positively towards the East, and y-values increased positively towards the North (Fig. 10). For example, the starting coordinates for line 1 in a large gap for both North and South directions would be (0, 1) and (0, -1), respectively.

Centered on the baselines, 1m wide sampling strips were established for measuring seedlings, vegetation and microsite types (Fig. 10). At 2m intervals along the sampling strips, these were assessed on square plots (quadrats), each measuring $1m^2$ (1m x 1m). In the field, a plastic frame with 10cm markings along its length was used to define the quadrat; the frame was moved along the length of the sampling strip as analyses proceeded (Fig. 11). Each quadrat on the baseline was numbered and its midpoint coordinates were recorded in meters, according to the coordinate system described in this section.

Figure 11. Sampling plot defined by $1m^2$ plastic frame on baseline at Isojärvi. *Photo credit:* Margot Downey

Centered on the baselines, 21m wide sampling strips were established for measuring trees, windthrows and windsnaps (Fig. 10). These strips extended 10m beyond all of the seedling/vegetation/microsite sampling strips into the residual forest stand.

For each gap, the following general identifiers were also recorded: treatment block (I50, S90 etc.), stand (Metsähallitus stand ID, e.g., 146) and gap ID (e.g., 146.3), strip number (1, 2 in small gaps; 1, 2, 3, 4 in large gaps), measurement team, and date. An overview of gaps and their relevant characteristics are outlined in Table 1 below.

Table 1. Gap and sampling overview for the 2014 DISTDYN field measurements at Isojärvi

Treatment block	Stand	Site type	Gap ID	Gap area (ha)	Gap size	Sampling strip orientations			
S50	40	MT	40.1	0.15	small	N	S	E	W
S50	40	MT	40.2	0.19	small	N	S	E	W
S50	41	MT	41.1	0.21	large			E	W
S50	42	OMT	42.5	0.13	small	N	S	E	W
S90	73	OMT	73.5	0.17	small	N	S	E	W
S90	77	MT	77.2	0.12	small	N	S	E	W
S90	77	MT	77.3	0.13	small	N	S	E	W
S90	89	MT	89.3	0.15	small	N	S	E	W
I90	100	MT	100.4	0.36	large	N	S	E	W
I90	112	MT	112.1	0.33	large	N		E	W
I90	115	OMT	115.2	0.18	large	N	S	E	
I90	118	MT	118.1	0.18	large	N		E	W
I90	118	MT	118.2	0.16	large			E	W
I90	118	MT	118.3	0.21	large	N	S		
I50	129	MT	129.2	0.20	large	N		E	W
I50	146	MT	146.3	0.10	small	N	S	E	W
I50	151	MT	151.1	0.22	large	N	S	E	W
I50	151	MT	151.3	0.17	large		S		W

3.2.3. Seedling measurements

Within the $1m^2$ quadrats, all seedlings with a height of <500cm were recorded. Functionally similar seedlings (of the same species, of approximately the same age, height and vigor) were recorded as a group. For each individual or group of seedlings, the following was recorded:

- Seedling (or group) number (running number for all seedlings on the strip)
- Species: 1 = Scots pine (*Pinus sylvestris* L.),
  2 = Norway spruce (*Picea abies* (L.) Karst.),
  3 = silver birch (*Betula pendula* Roth.),
  4 = pubescent birch (*Betula pubescens* Ehrh.),
  5 = European aspen (*Populus tremula* L.),
  6 = grey alder (*Alnus incana* Moench),
  7 = common alder (*Alnus glutinosa* L.),
  8 = other conifer,
  9 = other broadleaf.
- Height (in cm); for groups of seedlings, the height recorded was the mean height for the group

- Vigor: 1 = Good, 2 = Weak, 3 = Dead
- Total number of seedlings in the group (1 for an individual)
- Whether or not the seedling had emerged after the gap harvesting treatment (1 = Yes, 0 = No)

3.2.4. Vegetation measurements

Within the same $1m^2$ quadrats, the total percent covers of vegetation species groupings were assessed by ocular estimation. The percentage cover was estimated by classes of 0.1% increments from 0–1%, and of 1% increments (1%, 2%, 3%, etc.) above 1%. Species groupings included: shrubs (e.g., *Rubus idaeus, Juniperus communis, Ribes spp., Lonicera xylosteum, Frangula alnus, Amelanchier spicata,* and *Salix* species — except *S. caprea* and *S. pentandra*), dwarf shrubs (e.g., *Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Calluna vulgaris, Empetrum nigrum, Ledum palustre, Andromeda polifolia, Arctostaphylos uva-ursi,* and *Chamaedaphne calyculata*), herbs, grasses/sedges, ferns, mosses and lichens.

Within some functional groupings, additional estimates were performed to assess the percent cover of a few species separately, each indicative of different site characteristics. These species were estimated in the same precision classes as the main groupings. They included: *Rubus idaeus* (shrub); *Calluna vulgaris*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea* (dwarf shrubs); *Epilobium angustifolium* (herb), *Calamagrostis* spp. (grasses); *Dicranum* spp., *Hyloconium splendens*, and *Pleurozium shreberi* (mosses).

3.2.5. Microsite and topography measurements

Within the same $1m^2$ quadrats, the percent cover of key microsite types were estimated also using ocular estimation techniques. Microsite types included: covered stone (by up to approximately 10cm of moss, humus, or soil), bare stone, logs (≥ 7cm diameter), bases of standing trees, bases of stumps, decayed stumps or logs, duff (leaves, branches, bark and other organic material, in various stages of early decomposition), slash (woody debris created during harvesting operations), bare mineral soil and bare humus. Cover was estimated by classes of 1% increments. The dominant topography type of the quadrat was also recorded. Topography types were: flat (or somewhat undulating), sloped, depression, or mound.

3.2.6. Tree, windthrow and windsnap measurements

Within the 21m wide sampling strips, all standing trees with a height of ≥ 5m were measured, including standing dead trees and broken trees with a standing part > 1.3m high. The record for each tree included: its species, number (a running number for all standing trees at the gap), two measurements of diameter, coordinates, and strip number (1, 2, 3, or 4). Tree diameters were measured at breast height (1.3m) using a caliper, were taken from two perpendicular directions, and were recorded in mm. Coordinates were measured in cm using a clinometer and measuring tapes placed along the baselines, according to the four-strip system described in Section 3.2.2 for large gaps. Additional information on the trees' health, vigor, and damages was recorded under "Notes".

In some gaps, the trees (>5m in height) had already been measured by Luke (Metla at the time) 4 years before. In these gaps, no new tree measurements were made. However, all damaged or broken trees were noted, and coordinates were taken to compare to the previous records. Based on both current and previous records, the basal area of all standing trees was calculated for all species measured in the residual forest stand of each gap. These values along with some highlights of the residual stands' species composition are shown in Table 2 below.

Table 2. Characteristics of the residual forest stands at Isojärvi

Gap ID	Measurement year	Basal area (m^2 ha^{-1})	Norway spruce (%)	Birch spp. (%)	Scots pine (%)
40.1	2010	26	42	36	5
40.2	2010	24	50	33	8
41.1	2010	32	85	5	10
42.5	2014	24	36	34	13
73.5	2010	26	75	17	6
77.2	2010	23	73	24	1
77.3	2010	25	71	18	2
89.3	2014	21	82	14	2
100.4	2014	24	56	28	10
112.1	2014	29	34	13	53
115.2	2010	18	55	4	2
118.1	2014	24	11	19	15
118.2	2014	23	18	21	51
118.3	2014	22	28	12	36
129.2	2014	19	46	6	43
146.3	2010	21	81	14	0
151.1	2014	23	82	15	3
151.3	2014	21	59	23	4

Within this same 21m wide sampling strip, windthrows and windsnaps were measured. Windthrows are defined as entire trees downed and uprooted during a disturbance event, usually by strong winds and storms (an example is shown in Fig. 12). When trees are broken somewhere along their trunk, they are called windsnaps. The record for each windsnap or windthrow included: its species, number (a running number for all windthrows/windsnaps at the gap), diameter class (1 = 0–10cm, 2 = 10–20cm, 3 = 20–30cm, etc.), coordinates, and strip number (in the same system as for trees).

Figure 12. Windthrows inside gap at Isojärvi. *Photo credit:* Margot Downey

3.3. Data analysis

For this study, all data transformations, exploration, analyses and visualizations were performed using the statistical software R, version 3.1.2 (R Core Team 2014). Several packages were installed in R in order to access a variety of additional statistical and computational functions. The format of the data matrices were manipulated for different purposes throughout the entire data analysis process using the "plyr" package (Wickham 2011). To convert these transformed matrices into new Excel tables, the package "xlsx" was used (Dragulescu 2014). All plotting of raw data was supported by the "lattice" package (Sarkar 2008). Statistical summaries of the raw data were found using the "psych" package (Revelle 2015). Analyses of variance were performed using "car" package (Fox and Weisberg 2011) along with the base functions available in R. Lastly, the generalized additive models were created using the "mgcv" package (Wood 2011), and the model response variables were plotted using the "plotmo" package (Milborrow 2015).

3.3.1. Data processing

In the data transformation phase, all seedling and vegetation baselines were standardized by labeling them as either N, E, S or W strip (4 strip possibilities in all gap sizes). For modeling purposes in R, the 4-strip labeling system (clockwise from 1 = North) was used, where the

class number variable was defined as a factor. Distances from gap edge were standardized for both small and large gaps; baseline center (0, 0) was defined as the gap edge, with increasing (positive) distance values towards the gap center and decreasing (negative) values into the residual forest (Fig. 13). The baselines for the tree measurements were left in the original sampling coordinate system (Fig. 10).

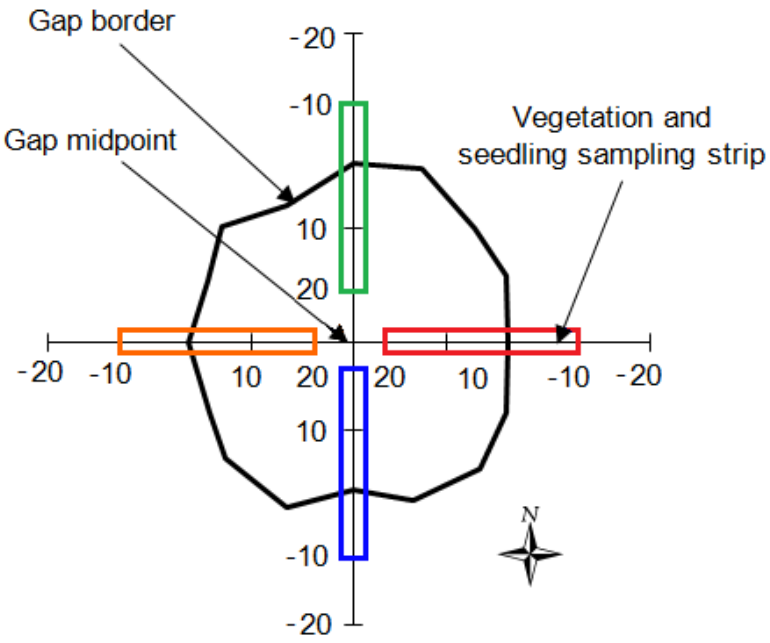


Figure 13. Coordinate system for all gaps after data transformation phase.

In R, the variables of Strip orientation, Gap ID, Stand, and Topography were all set as factors; all distance from edge and percent cover variables (vegetation and microsite types) were set as numerical values.

3.3.2. Data exploration

In the first phase of the data exploration process, the digitized data were checked for any inconsistencies and outliers. If such a value was found, the original field measurement booklet was consulted to check if it had been entered incorrectly into the computer file. Data consisting of numerical variables were checked by creating dot plots for the response variables (number of seedlings per m^2 by species) and for all explanatory variables (percent cover of vegetation and microsite types).

In the second phase, the data were checked for the presence of collinearity between the explanatory variables. For the factor type variables (topography, strip orientation), conditional boxplots were generated for these against all other numerical variables and visually assessed for the presence of patterns; boxes aligned horizontally on the plot indicated that no collinearity problems existed. In the case of continuous numerical variables, a matrix of scatterplots for all variables was made and visually assessed for patterns. Next, Pearson's correlation coefficients ($\rho_{X,Y}$) were calculated for each numerical variable against the rest (where values close to +1/-1 indicate a high degree of correlation/anticorrelation). This was done according to Equation 1 below, where cov(*X*,*Y*) indicates the covariance between *X* and *Y*, where *E* is the expected value (probability-weighted average for all possible values), and where σ and μ are the standard deviation and mean for *X* and *Y*, respectively.

$$\rho_{X,Y} = \operatorname{corr}(X,Y) = \frac{\operatorname{cov}(X,Y)}{\sigma_X \sigma_Y} = \frac{E[(X-\mu_X)(Y-\mu_Y)]}{\sigma_X \sigma_Y} \qquad \textbf{Eq. 1}$$

During the modeling phase, results from the collinearity diagnostics were used to inform the manner in which the variables were entered into the models. Most importantly, each of the potentially collinear variables was entered separately in the models during the model exploration process. If two collinear variables were statistically significant in the model, the choice of which covariate to keep was based on their degree of statistical significance and/or on their ecological significance according to the literature.

To check for problems related to zero-inflated count values for the number of seedlings per m^2, frequency plots were generated for each tree species, both for the total number of seedlings and separately only for the seedlings which emerged after harvest.

3.3.3. Analyses of variance

To test for the influence of categorical variables (strip orientation and topography) on the mean number of seedlings and the mean percent cover of key vegetation species per m^2 (plot), analyses of variance (ANOVA) were performed on the raw data. Strip orientations represent the plot's position in the gap, and are explained by Figure 13 (above). Topography represented the dominant relief category at the plot level (m^2), either flat, slope, depression (pit) or mound. The influence of strip orientation and topography on the means was checked

for the entire length of the sampling strips (from the inner gap into the residual forest), and then separately only for plots which were located inside the gap.

The first step was to test whether or not the data were normally distributed. To do so, a quantile-quantile (q-q) plot was created and assessed visually for patterns. Points deviating from the central q-q line would indicate non-normality in the data. The second step was to test the validity of the hypothesis that the groups to be tested had equal variances. For this, the Levene test was performed on the total seedling number per m^2 and the percent vegetation cover values according to the classes of the categorical variables. If the Levene test showed that $p>0.05$, then the hypothesis was not rejected. It should be noted that there was an equal number of values within all the different groups.

If both these steps produced satisfactory results (fairly normally distributed data, and equal variances), then a one-way analysis of variance was performed for each seedling species and vegetation cover type according to the classes of the categorical variables. If a significant difference between the groups was detected ($p<0.05$), this was followed by Tukey's post-hoc test to identify where the differences lay.

If the data appeared to be non-normally distributed, either a logarithmic transformation was applied before the previous tests, or the non-parametric Kruskal-Wallis one-way analysis of variance by ranks was applied instead. The non-parametric approach was also taken if the data groups had unequal variances. If a significant difference between the groups was detected ($p<0.05$) with the Kruskal-Wallis test, boxplots were constructed for each group of values and visually inspected to discern where the significant difference lay. In many cases, since the data were not perfectly normally distributed, these steps were applied in addition to the one-way ANOVA and Tukey's post-hoc test in order to make the original conclusions more robust.

This information was later used during the modeling phase to help direct investigations on the way the explanatory variables should be entered into the models. This was mainly done by adding the categorical variable in question as an influential factor to any continuous covariate for which a significant influence was detected (for example, see Eq. 7 in Section 4.3.2).

3.3.4. Modeling relationships

Models were created to relate the series of explanatory variables (covariates) to the mean number of seedlings per m^2 of both Norway spruce (*Picea abies* (L.) Karst.) and birch species (*Betula pendula* Roth., *Betula pubescens* Ehrh.). Models were created for seedlings of all ages, and then separately only for those which emerged after harvest (<5 years of age). Possible explanatory variables included residual stand basal areas for each gap (Table 2), percent covers for all microsite and vegetation types, along with the categorical variables of sampling strip orientation (N, S, E, or W) and dominant plot-level topography.

To model the relationships between the mean number of seedlings and explanatory variables, generalized additive models (GAMs) were used because the data were found to have non-linear forms (Wood 2006). The non-linearity of the data was revealed by first creating a linear model explaining the mean number of seedlings per m^2 of each species by a set of significant covariates. The residuals of these linear models were then themselves modeled in GAMs, as explained by the same covariates used in the linear models (this time with smoothing functions applied). In these GAMs explaining the residuals of the linear models by the same covariates smoothed, some covariates had estimated degrees of freedom (edf) > 1, suggesting that they were non-linearly related. The example model summary shown below is for the GAM that fits the residuals of the linear model explaining the number of birch seedlings per m^2 that emerged after harvest (LinResid), as a function of a set of covariates. In this GAM's summary, it is clear that the distance from gap edge (Dist.) and the percent cover of young stumps and decayed stumps are non-linearly related to residuals of the linear model (LinResid).

```
Family: gaussian
Link function: identity

Formula:
LinResid ~ factor(Strip) + s(Dist.) + s(dwarf.shrubs) + s(grasses) +
    s(young.stumps) + s(decayed.stump.log) + s(Basal.area)

Parametric Terms:
              df     F p-value
factor(Strip)  3 0.051   0.985

Approximate significance of smooth terms:
                       edf Ref.df     F  p-value
s(Dist.)             6.459  7.601 5.244 3.81e-06
s(dwarf.shrubs)      1.000  1.000 0.113   0.7365
s(grasses)           1.000  1.000 0.442   0.5062
s(young.stumps)      8.619  8.951 4.296 1.87e-05
s(decayed.stump.log) 2.184  2.706 3.238   0.0266
s(Basal.area         1.000  1.000 0.026   0.8712
```

Moreover, the mean number of seedlings per m^2 across the entire sampling strip follows a fairly complex non-linear pattern which cannot be easily linearized by applying common polynomial functions (cubic, quadratic, etc.). This supports results from previous studies discussed in Sections 1.2 and 1.3, which found that when a distance gradient from inner gap to inner forest is considered, the density of seedlings often show non-linear patterns. Furthermore, the position in the gap, vegetation cover, topography and microsites generally had complex effects on the number of seedlings present.

GAMs are particularly useful tools for attempting to uncover the relationships between variables, whether they are near-linear, polynomial or more complexly non-linear. In addition, GAMs allow each of the covariates to be entered into the model with their own unique functions. Equation 2 below describes this relationship, where $f_i(x_i)$ represents the various unique functions of the p number of covariates, and $E(Y)$ the model's estimated fitted values (in this case, the estimated number of seedlings per m^2). It should be noted that GAMs can also create linear functions; however, when the use of GAMs is justified it is because some (but not necessarily all) of the covariates enter in a non-linear way. In GAMs, these functions are determined non-parametrically or semi-parametrically and take the form of "smooth functions" which are estimated through non-parametric methods.

$$g(E(Y)) = \beta_0 + f_1(x_1) + f_2(x_2) + \ldots + f_p(x_p) \qquad \textbf{Eq. 2}$$

The models were created using the gam() function of the "mgcv" package in R; Equation 3 below indicates the basic script for coding Equation 2 in R. Here, the choice of smooth functions ($s(x_i)$) was determined by the program through likelihood based methods or based on prediction error criteria. More specifically, these models used the "mgcv" package's default thin plate regression splines (TPRS) and cubic regression splines. The GAM then implemented a backfitting algorithm in order to combine these different methods to best estimate the appropriate function for each covariate.

$$\text{gam}(E(Y)) \sim s(x_1) + s(x_2) + \ldots + s(x_p), \text{ data} = mydata) \qquad \textbf{Eq. 3}$$

The distribution of the response variable in a GAM is assumed to fall under the exponential family (e.g., normal, Poisson, quasiPoisson, and negative binomial distributions). Within the gam() function in R, the family type (and thus the "link" function which relates the covariates to the response variable, $g(E(Y))$) can be specified in order to reach the best fit for the data. Setting the family type to reflect the Poisson distribution is typical for count-based response variables such as this. However, the observations for the number of seedlings per m^2 were slightly overdispersed (their variance exceeded the sample mean) with respect to the Poisson type distribution. In these cases, the negative binomial distribution can prove a useful alternative, since its additional parameters allow it to adapt to the variance independently of the mean. When using the negative binomial distribution, the variance function ($\text{var}(Y_i)$) assumed is defined by Equation 4 below, where μ_i is the fitted sample mean ($E(Y_i)$) and k is the aggregation parameter. In R this was coded as family=nb(), which is entered within the existing gam() function. The link function applied was the program default for the negative binomial distribution, the log link.

$$\text{var}(Y_i) = \mu_i + \frac{\mu_i^2}{k} \qquad \textbf{Eq. 4}$$

The covariate terms that best accounted for the variation in the response variable were selected through stepwise regression, by using a combination of the forward and backward elimination approaches. To do so, a GAM model was first created with a subset of the total possible covariates, chosen initially according to those that were deemed most influential in the literature. Based on ANOVA tables (printed in R using the anova() function), the covariate with the lowest p-value was eliminated and a new model fitted without it. This process continued until all covariates included in the model were statistically significant ($p<0.05$). However, in some cases covariates with larger p-values were kept in the model if they were otherwise deemed significant, e.g., based on the literature. Once this process was complete including only the most likely significant covariates, additional covariates were included in the model in the order of presumed highest relevance according to the literature.

Furthermore, to assess whether the deletion of a covariate term (and creation of a reduced model) was in fact an improvement on the original full model, the AIC test scores for both models were compared, using the R script AIC(model1,model2). If the reduced model (without the less significant covariate) showed an improved AIC score, then the backward

elimination process continued based on that model. However, if the original full model produced an AIC score that was better by a difference > 2, then this extra covariate was kept and the backward selection process continued by dropping the second least significant covariate instead. Therefore, a covariate was eliminated from the model only if it was deemed non-significant in the ANOVA tables, and if the AIC scores indicated that a model without it was a significant improvement on the model with it (full model). To further substantiate the decisions made based on these assessments, the deviance explained value for each model was also verified by consulting the model summaries. The final model included the smallest possible number of covariates while producing the lowest (best) AIC score and the highest possible deviance explained.

At this stage, boxplots were made showing this model's residuals against its fitted values for each group of the categorical variables (within topography and strip orientation). If patterns were visible, i.e. if there was a difference between the groups, then this categorical variable might have been influencing one of the continuous covariates. Based on the visual analysis of these boxplots and the results of the analyses of variance described in Section 3.3.3, categorical covariates (strip orientation or topography) were added as influential factors for some of the covariates where a significant influence was detected. When entered into the model in this way, a unique smooth function is created for the continuous variable according to the influence of each group of the categorical variable. If the inclusion of an influential factor in the smooth function of the covariate produced a model with an improved AIC as compared to the model without it, then this new model form was retained. In R, the influential categorical variable (e.g., x_2) is entered in the smooth function for the continuous covariate (e.g., x_1) by s(x_1, by = x_2). As a rule, if a covariate is an influential factor for another covariate in the model, it must also be entered separately as an independent covariate without a smoothing function.

The model validation process involved printing the standard diagnostic model residuals plots and information using the gam.check() function from the "mgcv" package. Also, the fitted values were plotted against the residuals in a separate plot and the patterns assessed, using resid(model) to find residuals, and fitted(model) to find the fitted values. Lastly, these model residuals were plotted against the observed values for each covariate. Any strong patterns in these plots, such as a significant deviation from an even spread about the horizontal zero residuals abline, would have signified a potential problem.

4. RESULTS

4.1. Data overview

There were 876 plots in total, and therefore 876 observations for all seedling, vegetation, topography and microsite types. The means, minimums and maximums for all variables measured in this study are listed in Table 3 below.

Table 3. Statistical overview of the study's variables

Variable*	Mean	SD	Median	Min	Max
Basal area	23.58	2.93	24.00	18.00	32.0
Norway spruce	2.07	5.49	0.00	0.00	71.0
After harvest	1.77	5.36	0.00	0.00	71.0
Germinants	1.38	4.15	0.00	0.00	59.0
Birch spp.	0.54	1.68	0.00	0.00	16.0
After harvest	0.37	1.35	0.00	0.00	15.0
Germinants	0.12	0.78	0.00	0.00	13.0
Shrubs	9.23	19.72	0.00	0.00	98.0
Rubus idaeus	9.17	19.63	0.00	0.00	98.0
Dwarf shrubs	11.37	14.30	6.00	0.00	77.0
Calluna vulgaris	0.15	1.26	0.00	0.00	23.0
V. myrtillus	6.85	9.84	3.00	0.00	74.0
V. vitis idaea	4.35	7.91	1.00	0.00	76.0
Herbs	7.73	11.55	4.00	0.00	94.0
E. angustifolium	3.21	9.35	0.00	0.00	89.0
Grasses	17.73	26.27	5.00	0.00	99.0
Calamagrostis spp.	13.69	22.29	3.00	0.00	99.0
Ferns	1.35	5.60	0.00	0.00	74.0
Mosses	45.88	32.53	39.50	0.00	100.0
Dicranum spp.	2.34	3.59	1.00	0.00	37.0
H. splendens	21.31	24.09	11.00	0.00	98.0
P. shreberi	16.98	19.43	9.00	0.00	96.0
Lichens	0.37	1.00	0.00	0.00	8.0
Covered stone	47.22	33.94	46.50	0.00	100.0
Bare stone	0.79	4.35	0.00	0.00	81.0
Tree base	0.72	3.59	0.00	0.00	49.0
Logs	5.59	8.75	0.00	0.00	68.0
Young stumps	0.80	2.58	0.00	0.00	26.0
Decayed stump	2.19	5.06	0.00	0.00	37.0
Duff	27.42	23.10	19.00	1.00	97.0
Slash	7.90	18.34	0.00	0.00	97.0
Bare mineral soil	0.06	1.37	0.00	0.00	40.0
Bare humus	0.35	2.47	0.00	0.00	58.0

***Note**:* Basal area is given in m^2 ha^{-1}, tree seedling values in number of individuals m^{-2}, vegetation and microsite values in % cover m^{-2}.

The mean number of seedlings per hectare inside the gap area were 20 360 (*Picea abies* (L.) Karst.) and 6 820 (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) (Table 3, given per m^2 plot). Of these seedlings, up to 62% were germinants (≤3cm). When considering only plots where seedlings were found, the average number of seedlings was approximately two times greater for Norway spruce, and four times greater for birch species. The greatest number of seedlings per m^2 occurred inside the gaps, in the 5–10m zone for Norway spruce and in the 0–10m zone for birch species (Fig 14). In the central gap positions (15m+ from the gap edge towards the gap center), there were 52% fewer seedlings per m^2 on average compared to the rest of the sampling strip (-10m to 15m). In this zone, the average number of plots without seedlings were 81% (birch) and 54% (Norway spruce) (Table 4 and Fig. 14).

Table 4. Mean number of seedlings per plot (m^2) with and without empty plots

	Norway spruce			Birch spp.		
Distance (m)	Mean	Mean (w/o empty)	% empty	Mean	Mean (w/o empty)	% empty
-9	2 ± 5	5 ± 8	57	0 ± 1	3 ± 2	95
-7	2 ± 3	4 ± 3	53	0 ± 1	2 ± 1	88
-5	2 ± 5	4 ± 6	52	0 ± 1	3 ± 3	95
-3	2 ± 5	5 ± 7	58	0 ± 2	8 ± 4	97
-1	2 ± 3	4 ± 4	52	0 ± 1	2 ± 2	82
1	2 ± 5	5 ± 5	48	1 ± 2	4 ± 3	80
3	2 ± 3	4 ± 4	50	1 ± 3	3 ± 4	67
5	5 ± 12	8 ± 15	42	2 ± 3	4 ± 3	65
7	3 ± 6	6 ± 8	52	1 ± 1	3 ± 2	77
9	3 ± 8	7 ± 11	58	1 ± 4	5 ± 9	78
11	2 ± 4	4 ± 5	57	0 ± 1	2 ± 1	72
13	1 ± 3	3 ± 4	68	1 ± 2	3 ± 3	75
15	1 ± 1	2 ± 2	71	0 ± 1	1 ± 0	79
17	1 ± 3	3 ± 4	51	0 ± 1	1 ± 1	85
19	1 ± 2	3 ± 3	60	0 ± 2	3 ± 3	85

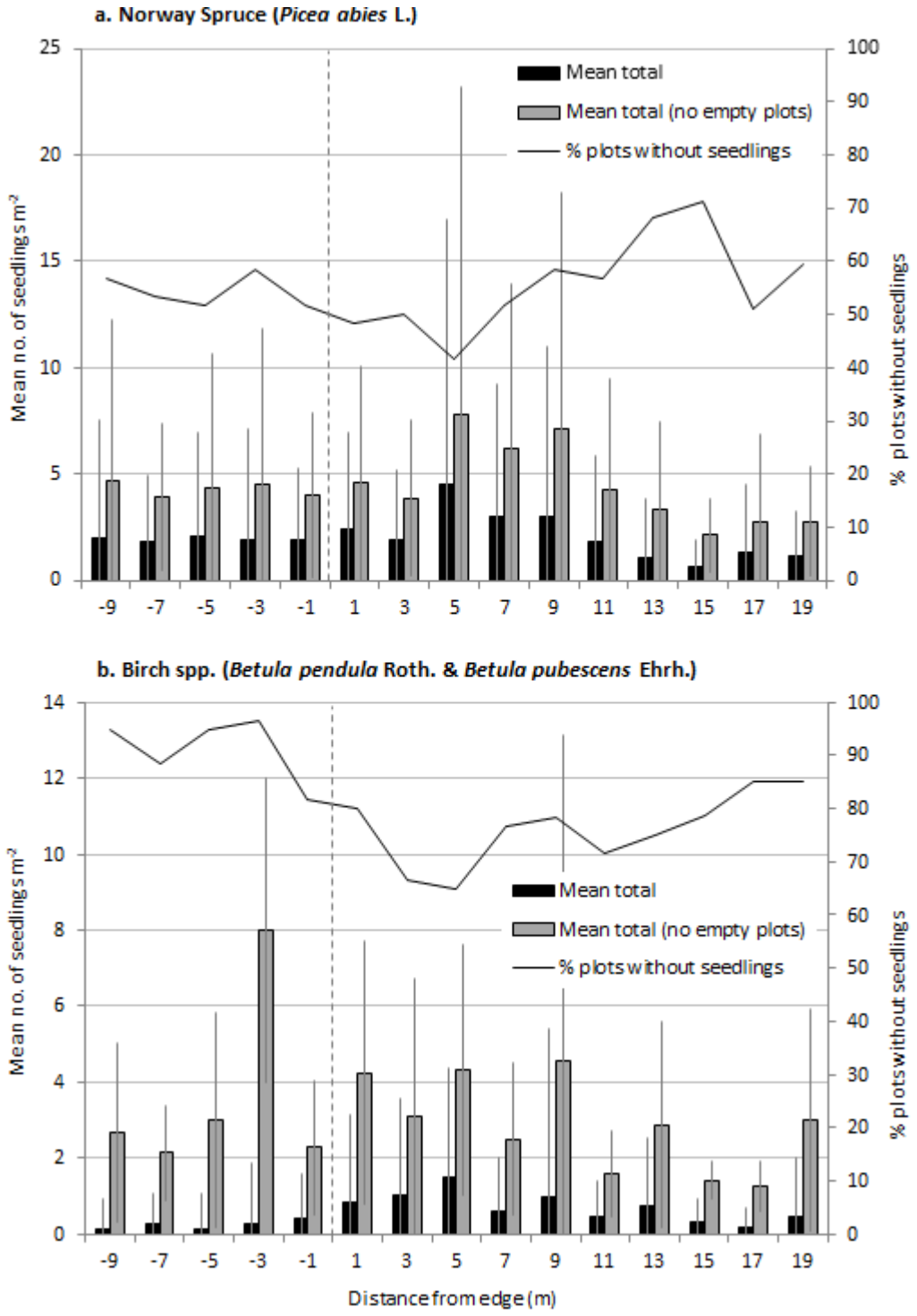


Figure 14. Mean number of seedlings in relation to gap edge

The 0–15m zone inside the gap supported the highest diversity of vegetation types (Fig. 15), and seedling species and abundance. The edge zone into the residual forest supported shade-tolerant vegetation species (dwarf shrubs, mosses). Gap centers (~15m+) promoted shade-intolerant vegetation species (grasses, shrubs, herbs), creating a highly competitive environment.

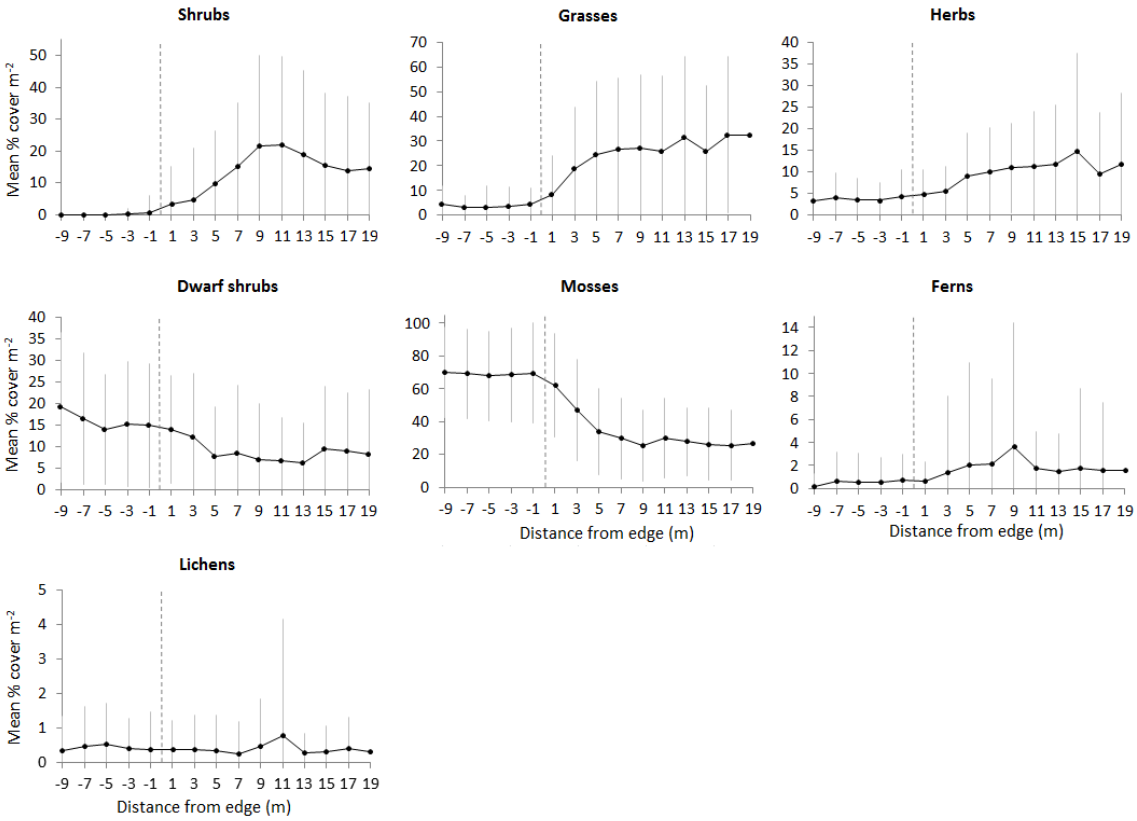


Figure 15. Mean percent cover of vegetation types as a function of distance

The mean basal area for the residual forest, accounting for the number of plots in each gap, was 24m^2 per hectare. The most common plot-level topography type was flat, followed by slope, mound and lastly by depression/pit. Of the 876 plots, the most commonly occurring microsite type was duff (Fig. 16). However, the microsite with the highest average percent cover was covered stone, followed by duff, then slash. The average percent covers of all microsite types were larger when considering only the plots where they occurred (excluding plots without that microsite type).

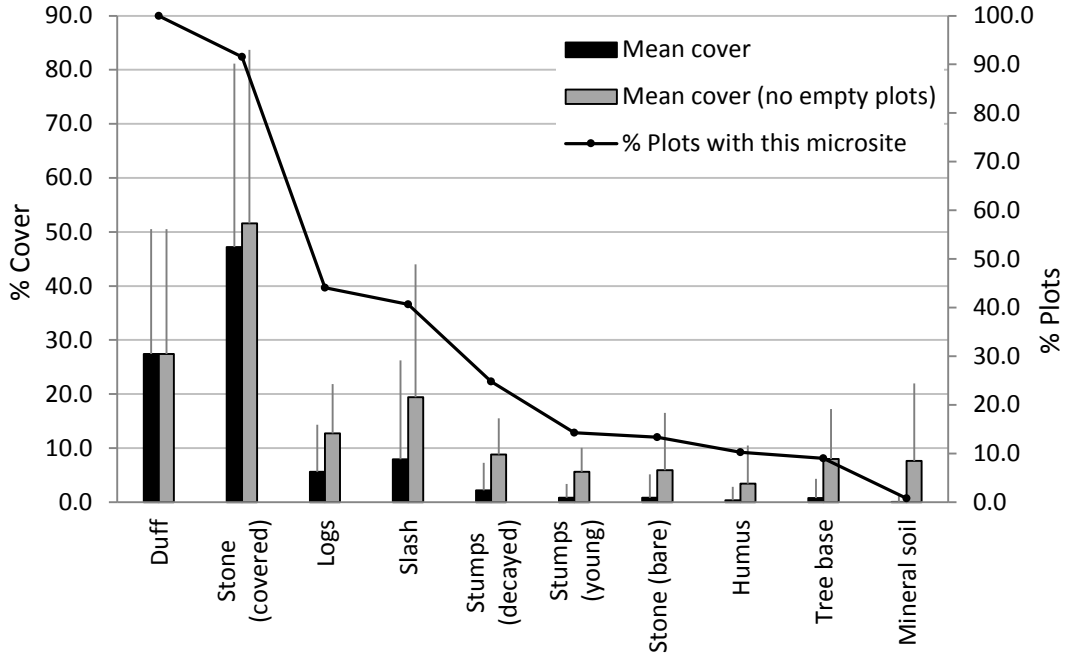


Figure 16. Mean percent cover and frequency for all microsite types

During the data exploration phase, the diagnostics of collinearity for continuous variables revealed relationships (Pearson's correlation values approaching ±0.5) between distance and mosses, grasses and mosses, and between mineral soil and bare stone (Appendices 1 and 2). These results were used to inform the modeling process, as described in Section 3.3.2. The diagnostics of collinearity for categorical variables revealed an effect of the position in the gap (strip orientation) on the percent covers of vegetation and microsite types (Appendices 3 and 4). The categorical variable of topography type appeared to have some effect on these variables as well (Appendices 5 and 6). These results suggested a need for analyses of variance on all the data categories.

4.2. Analyses of variance

The Levene test for checking the assumption of equal variance showed that the majority of the data within the categorical groupings did in fact have fairly equal variances ($p>0.05$). On the other hand, the quantile-quantile plots to test the assumption of normality showed that the majority of the data within the categorical groupings were not perfectly normally distributed (points deviated from the central q-q line). In many cases, transformations were not very successful at achieving normality in the data. For this reason, most of the analyses of variance relied on the non-parametric approach, where Kruskal-Wallis test values of $p<0.05$ signified

some form of significant variation among the means. In the case where the assumptions were met for the parametric approach, ANOVA values of $p<0.05$ were used to signify some form of significant variation among the means.

The results of the analyses of variance suggested that both the position in the gap (strip orientation) and plot-level topography influenced the mean number of seedlings and the percent cover of key vegetation species. However, the influence was only significant for certain species and varied among gap regions (entire sampling strips, or only plots in the gap interior).

Analyses on the influence of the strip orientation clearly revealed that the means of the northern (N) gap positions showed the most statistically significant differences when compared to means of the other positions (Fig. 17). When considering plots along the entire sampling strips, the N gap positions had significantly fewer birch seedlings (Kruskal-Wallis test $p = 0.046$ for all plots combined, and $p = 0.003$ including only plots inside the gap) and a significantly greater percent cover of dwarf shrubs (ANOVA test $p = 0.014$ for all plots combined, and $p = 0.001$ including only plots inside the gap). In addition, for the entire sampling strip, the N gap positions had a significantly smaller percent cover of ferns (Kruskal-Wallis test $p = 0.042$). However this effect was not statistically significant when tested only for the inner gap (Kruskal-Wallis test $p = 0.093$), indicating that the effect on ferns was more pronounced in the residual forest edge. When considering only the inner gap region, the N gap positions had a significantly greater percent cover of grasses than the other strip orientations (Kruskal-Wallis test $p = 0.017$). In summary, the N gap positions supported the growth of grasses and dwarf shrubs and limited the establishment and growth of birch seedlings and ferns.

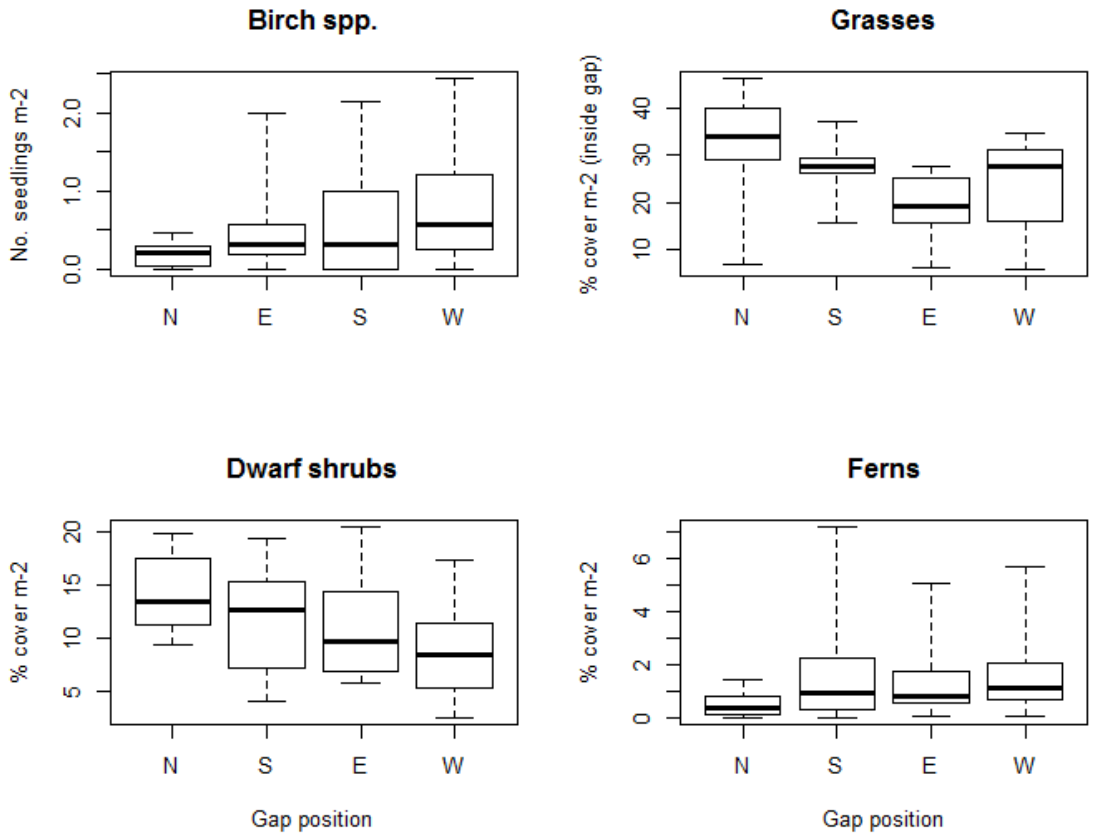


Figure 17. Means with significant variance between gap positions (North, South, East, West)

Analyses on the influence of plot-level topography clearly indicated that means for pitted topographies (depressions) and mounds showed the most statistically significant differences relative to means for the other topographies (Fig. 18). When considering plots along the entire sampling strips, depressions (pits) supported a significantly greater number of Norway spruce seedlings (Kruskal-Wallis test $p = 0.016$ for all plots combined, and $p = 0.011$ including only plots inside the gap), and a significantly lower percent cover of grasses (Kruskal-Wallis test $p = 0.025$ for all plots combined, and $p = 0.0005$ including only plots inside the gap). Mounds also supported a significantly lower percent cover of grasses when including the entire sampling strips. When considering only the inner gap region (lower two plots of Fig. 18), mounds had a significantly greater percent cover of mosses (Kruskal-Wallis test $p = 0.047$), and pits had a significantly lower percent cover of shrubs (Kruskal-Wallis test $p = 0.012$). In summary, pits promoted the establishment and growth of Norway spruce seedlings, and limited the growth of shrubs and grasses; mounds promoted the growth of mosses, and limited the growth of grasses. These effects were more pronounced in the gap interior.

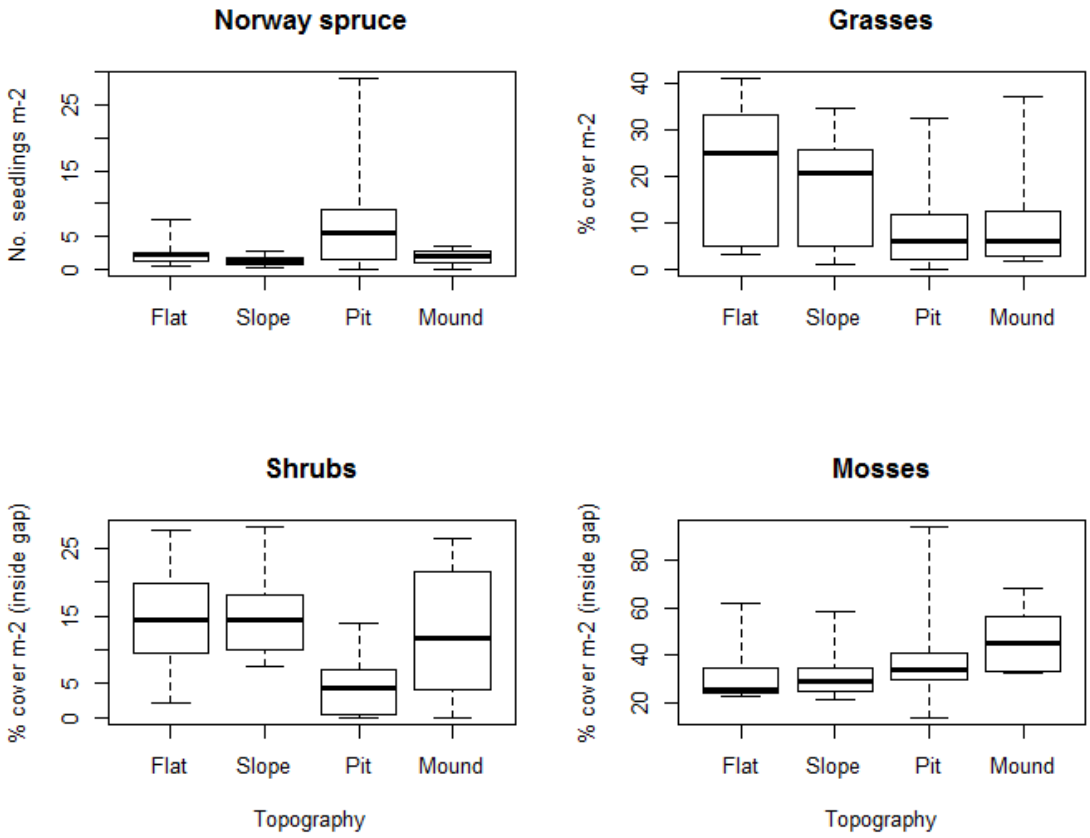


Figure 18. Means with significant variance according to dominant topography

4.3. The GAMs

4.3.1. Norway spruce

The final model estimating the number of Norway spruce seedlings per m^2 ($E(S)$) included several unique functions of covariates, according to Eq. 5 below. In the modeling process, the categorical variable of plot-level topography was found to have a significant influence on the overall magnitude of the relationships explaining the number of seedlings; each topography type modifies the magnitude of the intercept in this GAM.

$$g(E(S)) = \beta_0 + \beta(\text{Topo}_i) + f_D(\text{Distance}_i) + f_S(\text{Shrubs}_i) + f_{DS}(\text{Dwarf shrubs}_i) + f_H(\text{Herbs}_i) + f_G(\text{Grasses}_i) + f_{DF}(\text{Duff}_i) + f_{CS}(\text{Covered stone}_i) + f_{BA}(\text{Basal area}_i) \quad \textbf{Eq. 5}$$

According to the statistical model summary (Table 5), we can see that basal area—along with the percent cover of shrubs, dwarf shrubs, and covered stones—are linearly related to the

number of Norway spruce seedlings per m^2 in this model (estimated degrees of freedom, edf ≈1). On the other hand, the GAM detected a non-linear relationship between the number of seedlings per m^2 and distance, as well as the percent cover of herbs, grasses and duff (edf >1). All covariates are significant ($p<0.05$), aside from topography factor 'mound'. However, as a whole, topography is a significant covariate. It should be noted that the estimate for the intercept effect of flat topography ($\beta(\text{Topo}_{Flat})$) is included in the model intercept (β_0) in Table 5. This model explains 22.7% of the variance in the response variable. This model's diagnostic plots are shown in Appendix 7.

Table 5. Summary of the GAM for the number of Norway spruce seedlings per m^2

Parametric coefficients:				
	Estimate	*Std. Error*	*z value*	*Pr(>|z|)*
Intercept	0.36398	0.08204	4.437	9.13e-06 ***
$\text{Topo}_{\text{Slope}}$	-0.44209	0.16483	-2.682	0.00732 **
$\text{Topo}_{\text{Depression}}$	0.91687	0.31365	2.923	0.00346 **
$\text{Topo}_{\text{Mound}}$	0.19341	0.20702	0.934	0.35019
Approximate significance of smooth terms:				
	edf	*Ref.df*	*Chi.sq*	*p-value*
s(distance)	5.056	6.164	27.59	0.000136 ***
s(shrubs)	1.000	1.000	31.73	1.78e-08 ***
s(dwarf shrubs)	1.002	1.003	19.13	1.24e-05 ***
s(herbs)	3.829	4.675	14.46	0.010619 *
s(grasses)	2.911	3.602	50.45	3.57e-10 ***
s(duff)	2.792	3.483	9.79	0.031022 *
s(covered stone)	1.000	1.001	14.21	0.000164 ***
s(basal area)	1.001	1.001	13.73	0.000212 ***
Observations	876			
R-sq.(adj)	0.154			
Deviance explained	22.7%			

Note: ∗p<0.05; ∗∗p<0.01; ∗∗∗p<0.001

Figure 19 shows the estimated number of Norway spruce seedlings as a function of the mean of all GAM covariates, fixed for a flat topography. A flat topography was chosen because it was the most frequent topography observation in the dataset and it produced the closest to mid-range estimated values as compared to the other topographies. Generally, the number of Norway spruce seedlings is negatively related to the percent cover of shrubs, dwarf shrubs, grasses, and covered stones, and positively related to basal area. The relationship with distance, herbs and duff is a bit more complex. As was discovered in the analyses of variances, this model predicts that the greatest number of Norway spruce seedlings occur in depressions (pits).

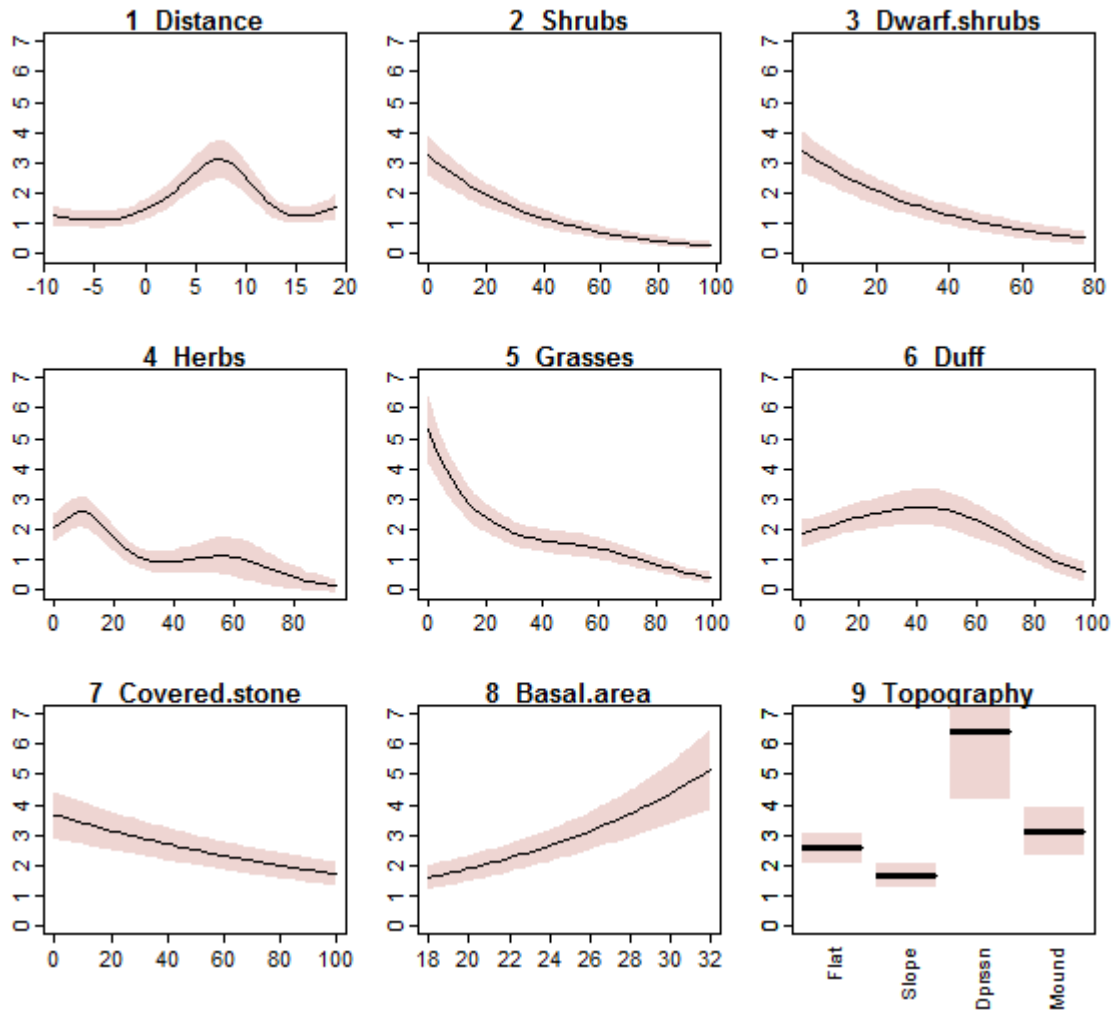


Figure 19. Estimated number of Norway spruce seedlings per m^2 as a function of GAM covariates. Shaded bands indicate the 95% confidence intervals.

The final model estimating the number of Norway spruce seedlings per m^2 which emerged only after harvest ($E(S_{AH})$) was similar to the model for all Norway spruce seedlings, however the percent cover of the microsite type 'duff' was no longer significant (Eq. 6).

$$g(E(S_{AH})) = \beta_0 + \beta(\text{Topo}_i) + f_D(\text{Distance}_i) + f_S(\text{Shrubs}_i) + f_{DS}(\text{Dwarf shrubs}_i) + f_H(\text{Herbs}_i) + f_G(\text{Grasses}_i) + f_{CS}(\text{Covered stone}_i) + f_{BA}(\text{Basal area}_i) \quad \textbf{Eq. 6}$$

According to the statistical model summary (Table 6), we can see that the percent cover of shrubs, dwarf shrubs, and covered stones is linearly related to the number of Norway spruce seedlings per m^2 in this model (edf ≈1). On the other hand, the GAM has detected a non-linear relationship between the number of seedlings per m^2 and distance, as well as the

percent cover of herbs and grasses, and a slightly non-linear relationship with basal area (edf >1). All covariates included in the model are significant ($p<0.05$), and the model explains 22.8% of the variance in the response variable. This model's diagnostic plots are shown in Appendix 8.

Table 6. Summary of the GAM for the number of Norway spruce seedlings per m^2 which emerged after harvest

Parametric coefficients:				
	Estimate	*Std. Error*	*z value*	*Pr(>|z|)*
Intercept	0.08117	0.09923	0.818	0.41338
$Topo_{Slope}$	-0.45819	0.19991	-2.292	0.02191 *
$Topo_{Depression}$	1.08783	0.37806	2.877	0.00401 **
$Topo_{Mound}$	0.50308	0.24699	2.037	0.04166 *
Approximate significance of smooth terms:				
	edf	*Ref.df*	*Chi.sq*	*p-value*
s(distance)	4.729	5.797	27.194	0.000122 ***
s(shrubs)	1.000	1.000	32.618	1.12e-08 ***
s(dwarf shrubs)	1.002	1.003	30.891	2.81e-08 ***
s(herbs)	3.579	4.396	11.526	0.028751 *
s(grasses)	2.854	3.530	46.215	2.32e-09 ***
s(covered stone)	1.000	1.000	20.321	6.56e-06 ***
s(basal area)	1.470	1.797	9.215	0.008566 **
Observations	876			
R-sq.(adj)	0.135			
Deviance explained	22.8%			

Note: $*p<0.05$; $**p<0.01$; $***p<0.001$

Figure 20 shows the estimated number of Norway spruce seedlings which emerged after harvest as a function of the mean of all GAM covariates, again fixed for a flat topography. Generally, the number of Norway spruce seedlings which emerged after harvest is negatively related to the percent cover of shrubs, dwarf shrubs, grasses, and covered stones, and positively related to basal area (as in the GAM for all Norway spruce seedlings). Again, the relationship with distance and herbs is a bit more complex. This model also predicts that the greatest number of Norway spruce seedlings occur in depressions (pits).

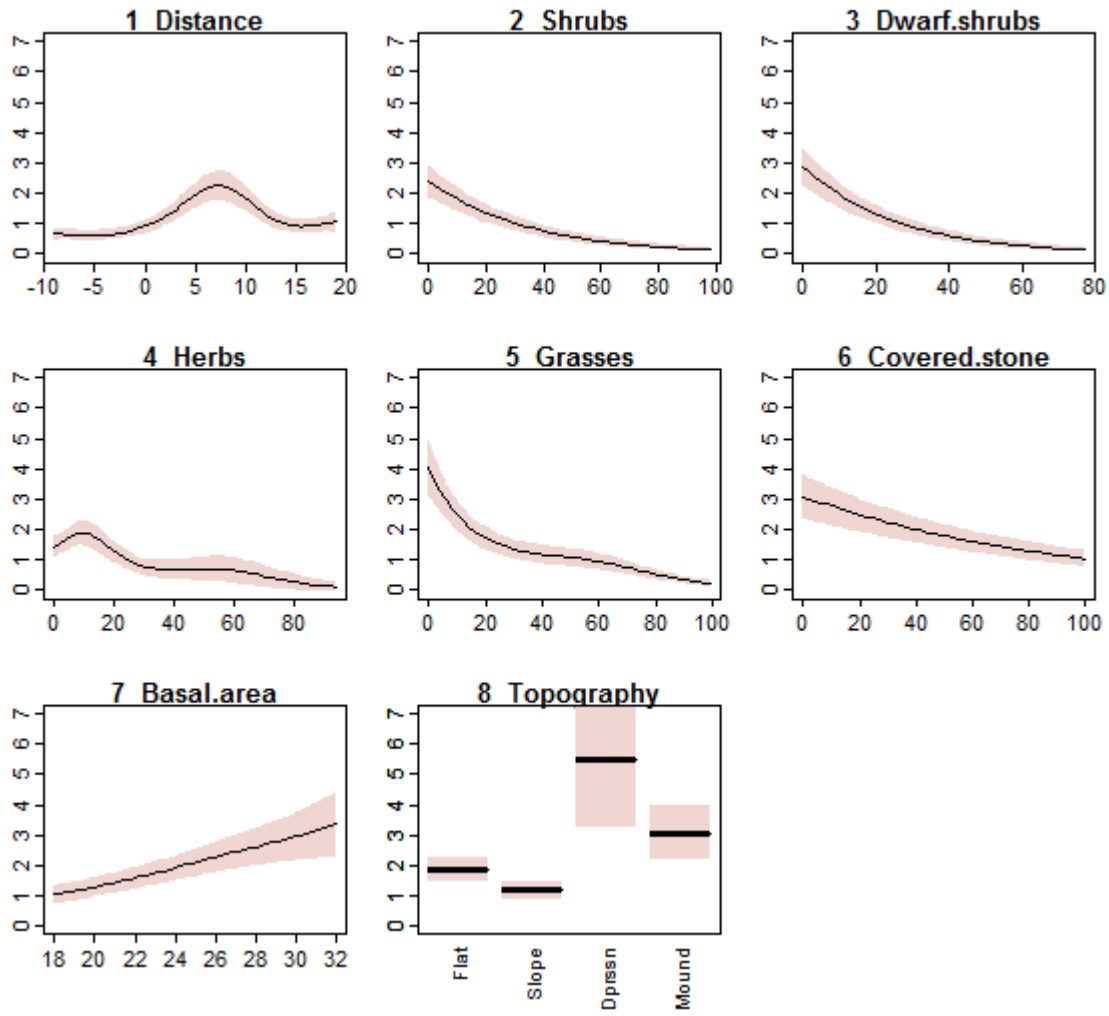


Figure 20. Estimated number of Norway spruce seedlings per m^2 which emerged after harvest as a function of GAM covariates. Shaded bands indicate the 95% confidence intervals.

4.3.2. Birch species

The final model estimating the number of birch seedlings per m^2 ($E(B)$) included several unique functions of covariates, according to Eq. 7 below. In the modeling process, the categorical variable of strip orientation (position in the gap) was found to have a significant influence on the overall magnitude of the relationships explaining the number of seedlings; in this GAM, each strip orientation type modifies the magnitude of the intercept (β_S). It also was discovered that the relationship between distance and the number of seedlings was also influenced by the position in the gap. Therefore, the distance-based function (f_D) of this GAM includes a separate smoothing function for each strip orientation ($S(i)$). The effect of each strip orientation on the distance-based function of the GAM can be seen in Figure 21, for all seedlings.

$$g(E(B)) = \beta_0 + \beta_S(\text{Strip Orientation}_i) + f_{D,S(i)}(\text{Distance}_i) + f_G(\text{Grasses}_i) + f_{YS}(\text{Young stumps}_i) + f_{DS}(\text{Decayed stumps}_i) + f_{BA}(\text{Basal area}_i) \quad \textbf{Eq. 7}$$

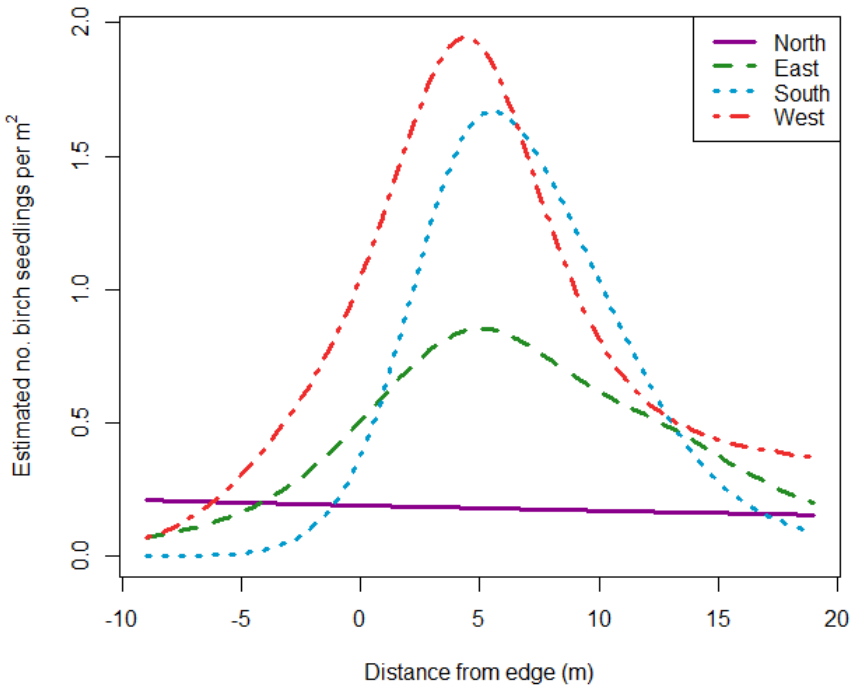


Figure 21. The estimated number of birch seedlings per m^2 as a function of distance from the gap edge, by strip orientation. Note: here, all other model covariates are set to their mean values.

According to the statistical model summary (Table 7), we can see that basal area, the percent cover of grasses, and distance in the northern gap positions are linearly related to the number of birch seedlings per m^2 in this model (edf ≈1). On the other hand, the GAM detected a non-linear relationship between the number of seedlings per m^2 and distance (for all other gap positions), as well as the percent cover of young and decayed stumps (edf >1). Figure 21 effectively displays these position-based relationships between the number of seedlings per m^2 and the distance from the gap edge. It should be noted that the estimate for the intercept effect of North strip orientation ($\beta(\text{Strip}_{North})$) is included in the model intercept (β_0) in Table 7. All covariates are significant ($p<0.05$), except for distance in the northern gap positions and basal area. However, as a whole, the interaction terms between strip orientation and distance are significant. Although basal area is not highly statistically significant in this model, it was deemed significant enough to include based on its proven effects in other studies. This model explains 28.5% of the variance in the response variable. This model's diagnostic plots are shown in Appendix 9.

Table 7. Summary of the GAM for the number of birch seedlings per m^2

Parametric coefficients:				
	Estimate	*Std. Error*	*z value*	*Pr(>|z|)*
Intercept	-1.8251	0.2333	-7.822	5.21e-15 ***
$Strip_{East}$	0.6760	0.3021	2.238	0.0252 *
$Strip_{South}$	-0.1159	0.5263	-0.220	0.8256
$Strip_{West}$	1.1489	0.2945	3.901	9.57e-05 ***
Approximate significance of smooth terms:				
	edf	*Ref.df*	*Chi.sq*	*p-value*
s(distance): $Strip_{North}$	1.001	1.002	0.141	0.707784
s(distance): $Strip_{East}$	2.954	3.686	13.343	0.007915 **
s(distance): $Strip_{South}$	3.477	4.346	20.143	0.000719 ***
s(distance): $Strip_{West}$	3.661	4.549	21.954	0.000402 ***
s(grasses)	1.000	1.001	6.378	0.011576 *
s(young stumps)	2.267	2.799	18.766	0.000289 ***
s(decayed stump)	2.202	2.733	13.212	0.003546 **
s(basal area)	1.000	1.000	0.261	0.609759
Observations	876			
R-sq.(adj)	0.0677			
Deviance explained	28.5%			

Note: ∗p<0.05; ∗∗p<0.01; ∗∗∗p<0.001

Figure 22 shows the estimated number of birch seedlings as a function of the mean of all GAM covariates, fixed for an eastern strip orientation. An eastern strip orientation was chosen because it produced somewhat mid-range estimated values as compared to the other strip orientations. Generally, the number of birch seedlings is negatively related to the percent cover of grasses, and only slightly positively related to basal area. The relationship with distance, young stumps and decayed stumps is a bit more complex. As was discovered in the analyses of variances, this model predicts the smallest number of birch seedlings in the northern gap positions.

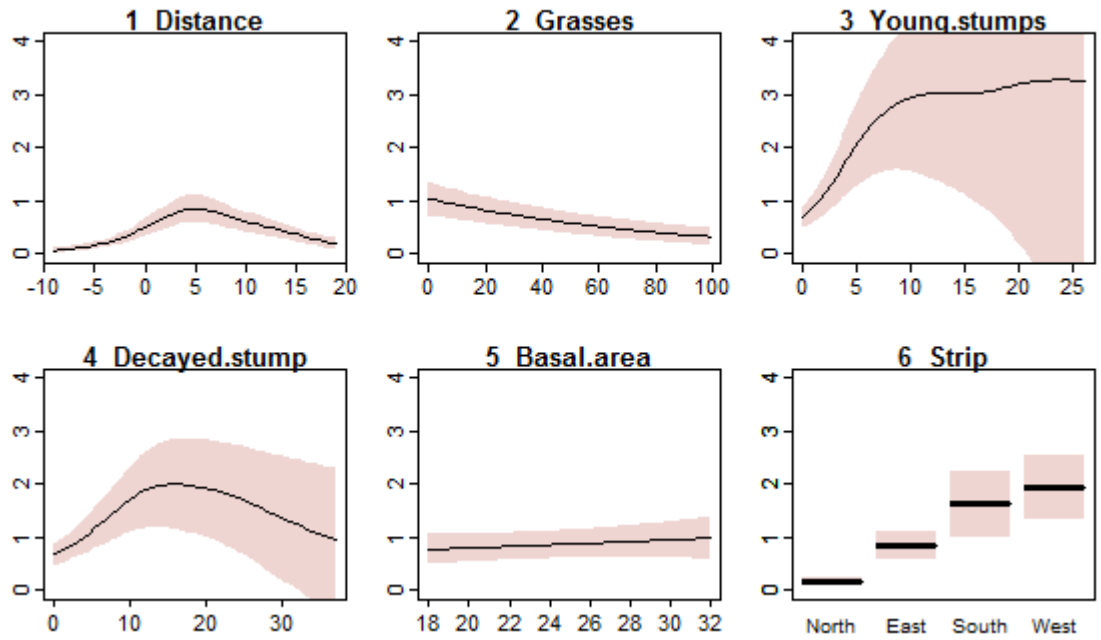


Figure 22. Estimated number of birch seedlings per m^2 as a function of GAM covariates. Shaded bands indicate the 95% confidence intervals.

The final model estimating the number of birch seedlings per m^2 which emerged after harvest ($E(B_{AH})$) was similar to the model for all seedlings, except that the percent cover of dwarf shrubs was significant (Eq. 8). Again, the categorical variable of strip orientation (position in the gap) was found to have a significant influence on the overall magnitude of the relationships on the number of seedlings, and was also found to influence the effect of distance. Therefore, strip orientation ($S(i)$) was again entered into this model as an influential factor in the distance-based function.

$$g(E(B_{AH})) = \beta_0 + \beta_S(\text{Strip Orientation}_i) + f_{D,S(i)}(\text{Distance}_i) + f_G(\text{Grasses}_i) + f_{DS}(\text{Dwarf shrubs}_i) + f_{YS}(\text{Young stumps}_i) + f_{DS}(\text{Decayed stumps}_i) + f_{BA}(\text{Basal area}_i) \quad \textbf{Eq. 8}$$

According to the statistical model summary (Table 8), we can see that basal area, the percent cover of grasses, dwarf shrubs, and young stumps, as well as distance in the northern gap positions are linearly related to the number of birch seedlings per m^2 in this model (edf $\approx$ 1). On the other hand, the GAM has detected a non-linear relationship between the number of seedlings per m^2 and distance (for all other gap positions), as well as the percent cover of decayed stumps (edf >1). Again, the estimate for the intercept effect of North strip orientation

($\beta(\text{Strip}_{North})$) is included in the model intercept (β_0) in Table 8. All covariates are significant ($p<0.05$), aside from distance in the northern gap positions, the percent cover of dwarf shrubs and basal area. As a whole, the interaction terms between strip orientation and distance are significant. The percent cover of dwarf shrubs was kept as a covariate since it produced a better AIC score (by a difference >2) than the model without it. Basal area was included in the model for the same reason described for the model predicting the number of all birch seedlings per m^2. This model explains 31.6% of the variance in the response variable. This model's diagnostic plots are shown in Appendix 10.

Table 8. Summary of the GAM for the number of birch seedlings per m^2 which emerged after harvest

Parametric coefficients:				
	Estimate	*Std. Error*	*z value*	*Pr(>|z|)*
Intercept	-2.2845	0.2819	-8.105	5.29e-16 ***
Strip_{East}	0.6415	0.3635	1.765	0.0776
Strip_{South}	0.2029	0.5586	0.363	0.7164
Strip_{West}	0.8285	0.3621	2.288	0.0221 *
Approximate significance of smooth terms:				
	edf	*Ref.df*	*Chi.sq*	*p-value*
s(distance): Strip_{North}	1.000	1.000	1.120	0.28994
s(distance): Strip_{East}	3.025	3.780	12.553	0.01190 *
s(distance): Strip_{South}	3.507	4.377	13.585	0.01218 *
s(distance): Strip_{West}	3.444	4.292	18.435	0.00143 **
s(dwarf shrubs)	1.689	2.122	5.693	0.06500
s(grasses)	1.001	1.003	3.854	0.04983 *
s(young stumps)	1.176	1.330	11.822	0.00136 **
s(decayed stump)	2.646	3.284	13.689	0.00471 **
s(basal area)	1.000	1.000	1.636	0.20085
Observations	876			
R-sq.(adj)	0.0877			
Deviance explained	31.6%			

Note: $*p<0.05$; $**p<0.01$; $***p<0.001$

Figure 23 shows the estimated number of birch seedlings which emerged after harvest as a function of the mean of all GAM covariates, again fixed for an eastern strip orientation. Generally, the mean number of birch seedlings which emerged after harvest is negatively related to the percent covers of grasses and dwarf shrubs, and only slightly positively related to basal area. The relationship with distance, young stumps and decayed stumps is a bit more complex. As with the model explaining the number of all birch seedlings, this model predicts the smallest number of seedlings in the northern gap positions.

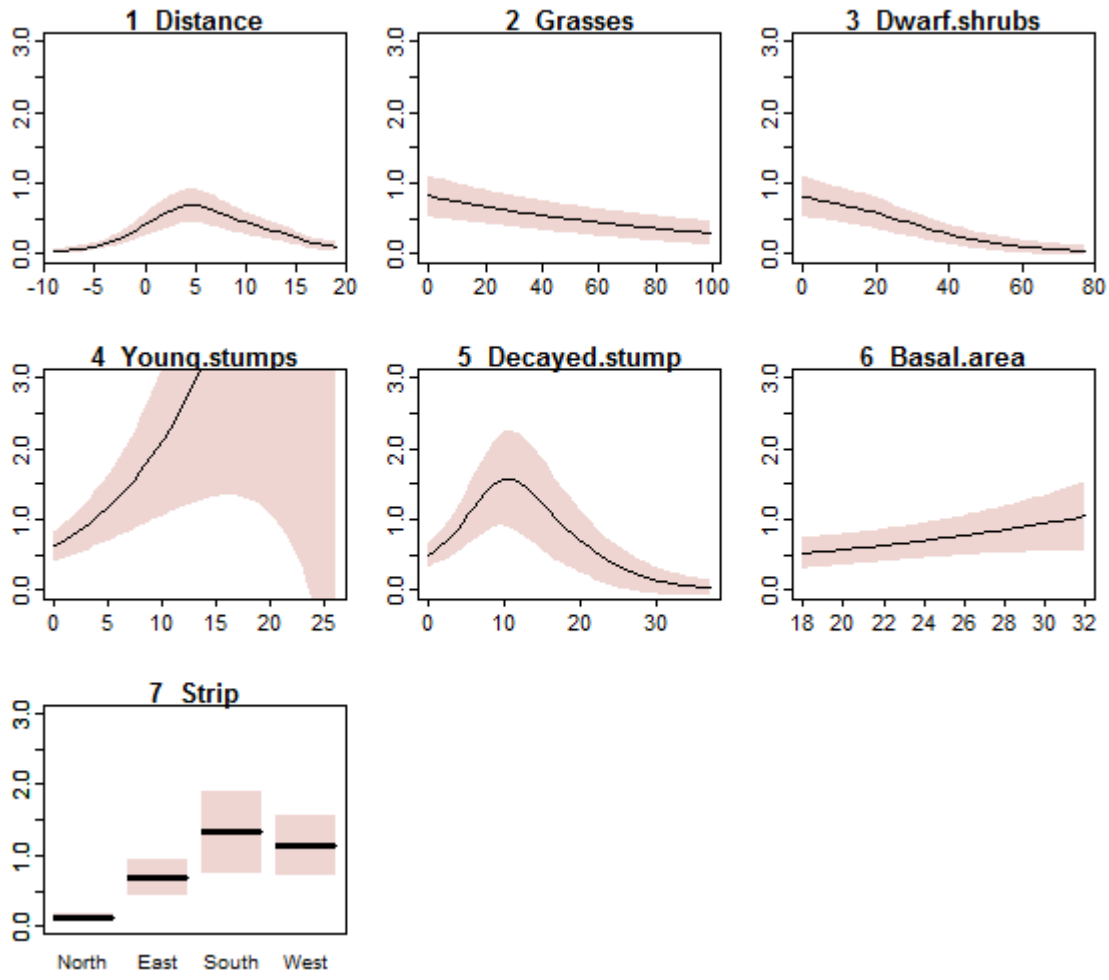


Figure 23. Estimated number of birch seedlings per m^2 which emerged after harvest as a function of GAM covariates. Shaded bands indicate the 95% confidence intervals.

5. DISCUSSION

5.1. The regeneration of Norway spruce

The variables which were the most influential for the natural regeneration of Norway spruce seedlings in the gaps were topography, distance from gap edge, basal area of the residual forest, and the percent cover of shrubs, dwarf shrubs, herbs, grasses, duff and covered stones. However, in the model for young seedlings (those which emerged after harvest, or within the past 5 years), the percent cover of duff was not significant. These results will be discussed in relation to existing research on the topic as well as with the results of other analyses presented in this study.

5.1.1. Effect of distance from the gap edge

Consistent with the hypotheses of this study, the distance from gap edge had a significant effect on the number of Norway spruce seedlings per m^2. Both the direct observations of this study and the GAMs showed very similar patterns in terms of the effect of the distance from gap edge on the mean density of Norway spruce seedlings. The patterns found were generally the same for all Norway spruce seedlings in this study, irrespective of their age.

Inside the residual forest stand, the number of Norway spruce seedlings per m^2 remained fairly stable with increasing proximity to gap edge. This differs somewhat from results of other studies, which found a slight increase in the density of spruce seedlings in the residual forest with increasing proximity to the gap edge (Burton 2002, Valkonen et al. 2011). The density of seedlings increased from the gap edge towards the gap interior; however, values remained fairly low within a distance of 5m from the edge. Taskinen et al. (2003) revealed that the negative effects of the edge trees would be the strongest within a distance of 5m from the edge. Their findings possibly explain the low number of spruce seedlings found in this region.

The highest spruce seedling densities occurred between 5–10m from the edge, revealing trends similar to those observed by Valkonen et al. (2011) and in line with this study's hypotheses. These results are also generally consistent with other studies, who found the greatest densities of spruce seedlings within the edge environments of the inner gap (Dai 1996, Burton 2002, Huggard and Vyse 2002a, Hanssen 2003, Valkonen et al. 2011). This is

likely because of the fact that these edge environments host lower levels of competition with other vegetation and receive a larger proportion of seeds from the mother trees, as discussed in Sections 1.2 and 1.3. Furthermore, since these regions remain partly shaded for much of the day, seeds and seedlings here would experience lower levels of evaporation and would have a greater likelihood of emergence and survival (Hanssen 2003).

From around 10m up to ~15m from the edge, the density of spruce seedlings decreased. Beyond a distance of 15m the density of spruce seedlings increased slightly; however, this may not be statistically significant considering the confidence intervals. Nevertheless, Hanssen (2003) also found a slight increase in Norway spruce seedling density within this distance from gap edge. One reasonable explanation lies in the fact that although spruce seedlings are shade tolerant, they tend to regenerate better in regions with greater light availability (Liu and Hytteborn 1991, Dai 1996). Generally though, the 15m+ region from the gap edge had fewer seedlings per m^2 and had the greatest percentage of plots without seedlings (Table 4 and Fig. 14) as compared to the rest of the sampling strip. This is likely attributable to greater levels of competition from vegetation in these regions (especially grasses, shrubs and herbs), as shown in Figure 15.

5.1.2. Effect of basal area

The basal area of the residual forest around the gaps in this study ranged from $18m^2\ ha^{-1}$ to $32m^2\ ha^{-1}$, and had an average of $24m^2\ ha^{-1}$. Basal area was entered into the models as an average value for each gap, since it was not possible to account for the different effect it had on plots situated within the residual stand and plots situated inside the gap. Therefore, the basal area values included in the models act only to scale the number of seedlings found across the entire measured gap region, and do not affect the plot-level seedling densities. As the model plots show (Figs. 19 and 20), an increasing basal area of the residual forest stand leads to greater average densities of Norway spruce seedlings in the gap and edge zones. This result is logical considering greater basal area values correspond to greater numbers of seed trees which surround the gap, leading to a greater likelihood of seeds falling and thus seedlings establishing in the gap and edge positions.

5.1.3. Effect of topography

The greatest density of Norway spruce seedlings occurred in depressions. This is in line with the study's hypotheses, since similar trends were observed in several other studies (Kuuluvainen and Juntunen 1998, Hanssen 2003, Kuuluvainen and Kalmari 2003, Diaci and Boncina 2005, Ilisson et al. 2007, Vodde et al. 2010). This trend likely reflects the fact that the heavy spruce seedlings preferentially accumulate in depressions/pits. Water and nutrients also accumulate in depressions, facilitating seedling germination and growth. Furthermore, depressions had significantly lower mean percent covers of shrubs and grasses, vegetation types which can be highly competitive with Norway spruce seedlings (Liu and Hytteborn 1991, Hanssen 2002, Hanssen 2003, Diaci and Boncina 2005, Valkonen and Maguire 2005, Kupferschmid and Bugmann 2005, Valkonen et al. 2011).

Contrary to hypotheses, the next greatest density of Norway spruce seedlings was found on mounds. However, these results are still consistent with many previous studies (Liu and Hytteborn 1991, Kuuluvainen and Juntunen 1998, Kuuluvainen and Kalmari 2003, Diaci and Boncina 2005, Pröll et al. 2015, Vodde et al. 2015). Since mounds have higher rates of drainage, they tend to be drier and host lower levels of competition. This was shown in the analyses of variance, where the cover of grasses was significantly lower on mounded topographies. Again, since grasses are proven as important competitors for resources with Norway spruce seedlings, by limiting competing vegetation mounds can therefore also favor the growth and establishment of seedlings. Additionally, analyses of variance showed that mounds promoted greater covers of mosses. Since mosses have moisture holding capacities, they are sometimes particularly good seedbeds (Liu and Hytteborn 1991, Hunziker and Brang 2005, Kupferschmid and Bugmann 2005) and support the growth of established seedlings (Kathke and Bruelheide 2010a). These reasons further explain the greater number of Norway spruce seedlings on mounds in this study. Thus, the results show that the positive characteristics of mounds largely outweighed their hypothesized negative effects on seedling density (especially for young seedlings).

Flat topographies supported the second lowest densities of Norway spruce seedlings in this study. Also, consistent with the hypotheses, sloped topographies supported the lowest seedling density. The analyses of variance revealed that flat and sloped topographies generally promote the growth of shrubs and grasses, thus creating high levels of competition

for resources. Furthermore, sloped topographies would also have greater drainage, and therefore have lower moisture levels. Since the germination and establishment of Norway spruce seedlings is known to be limited by low moisture levels (Bjor 1971, Skoklefald 1992b), and slopes had lower levels of mosses, the moisture limitation on sloped topographies likely explains the low numbers of seedlings measured on these topography types.

5.1.4. Effect of microsites

Covered stones were a significant microsite type for explaining the density of Norway spruce seedlings, regardless of their age. These results are in line with the study's hypotheses; however, the estimation that there would be a different effect for germinants and older seedlings was not observed here. In smaller percent covers, covered stones promoted higher than average Norway spruce seedling densities (e.g., by limiting the growth of competing vegetation). This is in line with findings from several other studies (Hytteborn and Packham 1987, Kupferschmid and Bugmann 2005, Valkonen and Maguire 2005). If the stones are significantly raised, they may also represent topographic mounds, and may therefore limit competing vegetation in favor of seedling regeneration, as described in Section 5.1.1. However, overall there was a negative and fairly linear relationship between the percent cover of this microsite type and the density of Norway spruce seedlings. A stony ground layer is generally characterized by surface undulations and therefore has greater drainage. Furthermore, because of their thinner surface layer, water retention on these microsites would also be limited. As a result, the moisture limitation associated with greater proportions of covered stones could significantly limit spruce seedling establishment and growth. This was reflected in the findings of Kathke and Bruelheide (2010b).

Duff was also a significant microsite type for explaining the density of Norway spruce seedlings. However, as hypothesized, duff-covered microsites were not significant for the seedlings which emerged after harvest (young seedlings). There was a nonlinear relationship between the percent cover of duff and the density of Norway spruce seedlings. While covers of 0–50% duff may have promoted the presence of Norway spruce seedlings, covers greater than this lead to a fairly rapid decrease in their density. These patterns are generally in line with this study's hypotheses. Several studies have found that duff can promote the establishment of Norway spruce seedlings (Hanssen 2002, Hanssen 2003, Hunziker and

Brang 2005), since it typically limits the growth of competing vegetation and has a higher nutrient content because of decomposing organic matter (Hanssen 2003). However, as the Norway spruce model and other studies suggest, larger (and likely thicker) duff covers are more often detrimental to spruce seedling establishment and survival (Nakamura 1992, Jeglum and Kennington 1993, Groot and Adams 1994, Pröll et al. 2015). Furthermore, the duff layers at Isojärvi are dominated by Norway spruce needles which are known to have allelopathic effects on vegetation and seedling growth (Gallet and Lebreton 1995). This presents another reason why significant covers of duff would limit the germination and growth of spruce seedlings.

Results did not reveal that stumps or logs were especially important microsites for the establishment of Norway spruce seedlings, as was hypothesized. This may be because of the higher levels of seedling mortality and lower growth rates reported for Norway spruce seedlings established on stumps and logs (Szewczyk and Szwagrzyk 1996, Kupferschmid and Bugmann 2005, Kathke and Bruelheide 2010b). Perhaps another explanation is the fact that these microsites were fairly uncommon in the gaps (Table 3).

5.1.5. Effect of vegetation

Shrubs, dwarf shrubs, herbs and grasses were the vegetation types which most significantly explained the density of Norway spruce seedlings, regardless of their age. As hypothesized, there was a negative linear relationship between the percent cover of shrubs and dwarf shrubs, and the density of Norway spruce seedlings. Because of the strong levels of competition exerted by shrubs on both above- and below-ground resources (Jäderlund et al. 1997), it is no surprise that these results are consistent with the trends described in the literature (Hanssen 2002, Hanssen 2003, Diaci and Boncina 2005, Valkonen and Maguire 2005, Kupferschmid and Bugmann 2005). Many studies have also highlighted the particularly negative effect of dwarf shrubs of the Ericaceae family on spruce seedling regeneration, explained by their various allelopathic effects (Pellissier 1993, Gallet 1994, Gallet and Lebreton 1995, Mallik and Pellissier 2000) and root mechanisms (Zackrisson et al. 1997). Since the dwarf shrubs present in these study sites largely belonged to the Ericaceae family, with highest percent covers of both *Vaccinium myrtillus* and *V. vitis-idaea*, these reported characteristics could significantly influence the success of Norway spruce seedling regeneration at Isojärvi.

Also, there was a nonlinear relationship between the percent cover of grasses and the density of Norway spruce seedlings. Grass covers of between 0–30% had a strong negative effect on the number of seedlings; between 30–100% covers, the effect was still negative but was much more moderate. Generally, these results agree with the hypotheses. Grasses are strong competitors for both below-ground (Moser 1965, Robic 1985, Hanssen 2003, Picon-Cochard et al. 2006) and above-ground resources (Harper and Macdonald 2002, Picon-Cochard et al. 2006). These reasons support the strong negative relationship seen in the model, trends which are broadly in agreement with previous research (Hertz 1932, Yli-Vakkuri 1963, Hanssen 2002, Hanssen 2003, Pages and Michalet 2003, Diaci and Boncina 2005, Kupferschmid and Bugmann 2005, Valkonen and Maguire 2005, Valkonen et al. 2011, Pröll et al. 2015). In addition, grass covers from 0–30% generally occurred in the gap edge zones (Fig. 13). Since the highest densities of spruce seedlings occurred in gap edge zones (Fig. 14), the effect of changes in the percent cover of grasses would be the most pronounced in these regions (and within this range of grass covers). Grass covers of 30–100% were generally found in more central gap positions, where spruce seedlings were consistently more seldom. These patterns support the model's conclusions that percent covers greater than 30% had a more moderate effect on the number of spruce seedlings.

Lastly, there was a nonlinear relationship between the percent cover of herbs and the density of Norway spruce seedlings. Smaller covers of herbs facilitated spruce seedling establishment. However, between 10–30%, herb covers had a strong negative effect the density of seedlings; this effect stabilized with midrange covers of herbs, and then began to strengthen with covers greater than 60%. The overall negative effect of herb cover on the density of spruce seedlings is consistent with the results described in the literature (Bell et al. 2000, Valkonen and Maguire 2005), and agrees with the hypotheses. The positive effect of small covers of herbs on the establishment of spruce seedlings might be explained by the ability of herbs to limit the growth of other competing vegetation, such as grasses and mosses. This is consistent with the results of Valkonen and Maguire (2005), who found that the presence of herbs was correlated with regions of greater seedling density. Since the herbs measured in this study varied greatly in terms of their morphological characteristics, their competitive strategies, as well as their spatial patterns growth across the gap, these differences may account for part of the non-linear patterns detected.

5.2. The regeneration of birch species

The variables which were the most influential on the natural regeneration of birch seedlings were cardinal position in the gap (strip orientation), distance from gap edge, basal area of the residual forest, and the percent cover of grasses, young stumps and decayed stumps or logs. For young seedlings (those which emerged after harvest, or within the past 5 years), the percent cover of dwarf shrubs was also a significant covariate in the model. These results will be discussed in relation to existing research on the topic, as well as with the results of other analyses presented in this study.

5.2.1. Effect of distance from the gap edge

Consistent with the hypotheses of this study, distance from the gap edge had a significant effect on the number of birch seedlings per m^2. Both the direct observations of this study and GAMs showed similar patterns in terms of the effect of distance from gap edge on the mean density of birch seedlings. The patterns found were generally the same for all birch seedlings in this study, irrespective of their age.

Inside the residual forest stand, the mean number of birch seedlings per m^2 was very low. For light-demanding birch species (Perala and Alm 1990a), these regions of low light intensity likely do not provide sufficient light resources for adequate seedling establishment and growth. This agrees with other studies, who have found that birch seedling regeneration is largely limited in shaded environments (Runkle and Yetter 1987, Liu and Hytteborn 1991, Busing 1994, Battles and Fahey 2000, Huth and Wagner 2006). Accordingly, the density of birch seedlings gradually increased towards the gap edge, and continued to increase up to a distance of 5m inside the gap. These findings are in line with results of other research, which found that birch seedling regeneration generally improved with increasing distance from the edge (Dai 1996, Valkonen et al. 2011).

From this local maximum at around 5m, the mean density of birch seedlings gradually decreased towards the gap center. These trends oppose the hypotheses of this study, which predicted greater densities of birch seedlings the central gap positions, irrespective of the greater levels of competition found there. For example, Valkonen et al. (2011) found that the number of birch seedlings steadily increased from gap edge to gap center. However, their results reflect the state of birch regeneration 10 years after harvest, which is twice as long as

the regeneration period of this study. On the other hand, Huth and Wagner (2006) studied the regeneration of birch seedlings within 5 years after harvest. As with the results of this study, they found very few birch seedlings in the central gap positions, explained by high levels of competition with grasses in these regions. Therefore, the results of this study confirm that in the central gap positions, the early regeneration success of birch seedlings is more affected by negative pressures of competition than positive influence of potential light resources. In the later regeneration phases, however, the spatial patterns may more closely reflect the availability of light resources across the gap, as found by Valkonen et al. (2011). This is discussed further in Section 5.3.4.

5.2.2. Effect of basal area

Again, basal area was entered into the models as an average value for each gap, since it was not possible to account for the different effect it had on plots situated within the residual stand and plots situated inside the gap. Therefore, the basal area values included in the models act only to scale the number of seedlings found across the entire measured gap region, and do not affect the plot-level seedling densities. As in the case of Norway spruce, the birch model plots (Figs. 22 and 23) show that an increasing basal area of the residual forest stand leads to slightly greater average densities of birch seedlings in the gap and edge zones. Again, this result is logical considering that greater basal area values correspond to greater numbers of seed trees surrounding the gap, which in turn leads to a greater probability of seedlings falling and establishing in the gap and edge environments.

Although basal area was not statistically significant in the birch seedling models, it was still included because it was considered to be meaningful. Perhaps birch seedlings are less affected by residual stand basal area than Norway spruce seedlings because of their reproductive mechanisms. Birch trees tend to produce large quantities of small and light seeds which are easily dispersed over relatively large distances (Sarvas 1948, Jonsell 2000, Wagner et al. 2004), and are therefore less directly affected by small variations in the number of seed trees surrounding the gap. To support this, the model plots show that older seedlings were much less affected by variations in the basal area (nearly no relationship between the variables), indicating that other factors played a much more critical role in determining the density of birch seedlings in the gap.

5.2.3. Effect of position in the gap

The lowest density of birch seedlings occurred in the northern gap positions. These results are contrary to the hypothesis, which estimated that there would be greater densities of birch seedlings in the northern gap positions because of the superior light levels found there (Canham et al. 1990). Therefore, a combination of other factors such as competition with vegetation, the influence of the edge stand or microsite types may play an even more important role in the patterns of birch seedling regeneration. This conclusion is supported by the results of Liu and Hytteborn (1991). Similarly, Friesen and Michaels (2010) found that pine growth in northern gap positions did not benefit from the greater exposure to light, signaling that other effects played a greater role in its regeneration. Lastly, in the northern gap positions, the effect of the distance from gap edge on the density of birch seedlings was linear and not significant ($p>0.05$). This further confirms that other site-level properties must have had a greater influence in the northern gap positions.

Other studies have reported a shift in the productivity and composition of understory vegetation towards the northern gap regions (Fahey and Puettmann 2008, Friesen and Michaels 2010). In this study, the northern gap positions supported significantly greater covers of grasses and dwarf shrubs, creating a highly competitive environment for the birch seedlings present there. Dwarf shrubs in particular were especially influential in the early stages of birch seedling establishment (for the seedlings which established after harvest). Therefore, the effect of the position in the gap likely differs whether seedlings are in early or late stages of establishment. The dynamics between birch seedling density and vegetation will be discussed further in Section 5.2.5.

Although the mean birch seedling densities were not significantly different in the other gap positions (E, W, and S), both the model and the boxplots of means show some notable differences. More specifically, they show greater birch seedling densities in the western and southern gap positions, and lower densities in the eastern gap positions. The fact that competition with vegetation plays a larger role in determining the establishment of birch seedlings in the early regeneration phase (Hartig and Lemke 2002, Huth and Wagner 2006) likely explains why the southern gap positions displayed greater densities of seedlings, even though these areas tend to have limited light exposure. The timing of the exposure to solar radiation is important in determining how seedlings can respond to the light. For example,

western gap regions receive the majority of solar radiation in the morning hours, when relative humidity is at its highest and air temperatures are at their lowest; these are the microclimatic conditions which are known to maximize the quality of birch seedling photosynthesis (Wayne and Bazzaz 1993a). Similarly, De Chantal et al. (2003) found greater conifer productivity in the western (and northern) gap regions. Therefore, vegetation as well as microclimatic variability among gap positions could potentially explain the greater densities of birch seedlings observed in the southern and western gap positions.

5.2.4. Effect of microsites

Both young and decayed stumps/logs were the most significant microsite types for determining the density of birch seedlings, regardless of their age. These conclusions are in agreement with the results of other research (Liu and Hytteborn 1991, Grenfell et al. 2011, Robert et al. 2012, Béland and Chicoine 2013), and with the hypotheses of this study. Furthermore, birch seedlings (especially *Betula pubescens* Ehrh.) are capable of regenerating from stumps by sprouting from basal buds (Kauppi et al. 1987, Perala and Alm 1990b), which also partly explains their relationship with this microsite type.

This study hypothesized that stumps and logs in more advanced stages of decomposition would be more favorable for seedling establishment and growth than younger ones, as was suggested by several studies (Kuuluvainen and Kalmari 2003, Zielonka and Piątek 2004, Zielonka 2006, Robert et al. 2012). However the results of this study do not validate this. Instead, the models predict lower densities on average on decayed vs. young stumps and logs. Some studies showed that since decayed stumps tend to be covered in thicker moss layers, the risk of drought for seedlings established there significantly increases (Hornberg et al. 1997, Zielonka and Niklasson 2001). This could explain the lower birch seedling densities encountered on these microsites. Additionally, Hofgaard (1993) found that young birch seedlings most commonly established on stumps in the earlier stages of decomposition. Since most birch seedlings in this study had established fairly recently, these results agree with this study's findings.

On average, there was an overall positive effect of the presence of decayed stumps and logs on the average density of birch seedlings. However, when decayed sump/log covers increased beyond 10–15%, this effect decreased in strength. Based on personal observations, it is speculated that this trend is linked to the often large covers of dwarf shrubs found on decayed

stumps and logs. Since the forests at Isojärvi are of *Myrtillus* and *Oxallis-Myrillus* Type, the dwarf shrubs had likely established on these microsites long before the gap was created. Research from spruce-dominated forests confirms that dwarf shrubs *Vaccinium vitis-idaea* and *V. myrtillus* are often the main vascular species occupying these microsites (Hofgaard 1993, Zielonka and Piątek 2004, Hautala et al. 2011, Kirchner et al. 2011). Although *Vaccinium myrtillus* is negatively affected by the removal of overstory trees (Kooijman et al. 2000, Jalonen and Vanha-Majamaa 2001), it can still persist for several years after harvest (Bergstedt and Milberg 2001). Since one of the principal favorable attributes of stumps and logs is that they tend to host lower levels of competition from understory vegetation (Sollins et al. 1987, Harmon and Franklin 1989), the presence of dwarf shrubs could have limited the potential positive effects of these microsite types on birch seedling establishment and growth, especially for those in the earlier stages of regeneration (Eq. 8).

5.2.5. Effect of vegetation

Grasses were the vegetation type most significantly related to the density of birch seedlings, regardless of their age. Dwarf shrubs were only significantly related to the number of birch seedlings which established after harvest. In accordance with the original hypotheses, grasses had a negative effect on the density of birch seedlings. Accordingly, the northern inner gap areas were dominated by grasses and had significantly fewer birch seedlings. This relationship is based on the fact that grasses exert strong competitive pressures on surrounding vegetation and seedlings, both for below-ground (Moser 1965, Robic 1985, Fanta and Kobus 1995, Hanssen 2003, Picon-Cochard et al. 2006) and above-ground resources such as light (Veer and Kooijman 1997, Harper and Macdonald 2002, Picon-Cochard et al. 2006). Other studies on early regeneration support this conclusion, in which sites occupied by grasses supported fewer birch seedlings on average (Hartig and Lemke 2002, Huth and Wagner 2006). Therefore, the models generally agree with the study's hypotheses that areas dominated by grasses would be expected to limit initial birch seedling regeneration. Again, perhaps as the regeneration process develops, the spatial patterns of birch regeneration in gaps would alter to reflect other factors of primary importance such as light resources.

Dwarf shrubs had a significant negative effect on the density of birch seedlings which emerged after harvest. Accordingly, the northern inner gap areas were also dominated by

dwarf shrubs and also had significantly fewer birch seedlings. These results support the initial hypotheses, and reflect the findings of other research (Gimingham 1984, Prévost et al. 2010). These results are largely attributable to the competitive abilities of shrubs for above-ground resources, as well as their allelopathic effects (Pellissier 1993, Gallet 1994, Gallet and Lebreton 1995) and competitive root mechanisms (Zackrisson et al. 1997). However, the presence of dwarf shrubs does not seem to be a significant factor for the older birch seedlings (>5 years old). This is likely because birch seedlings tend to grow fairly rapidly in height, and would soon exceed the dominant heights of dwarf shrubs. Therefore, competition for light resources from covers of dwarf shrubs would no longer be as strongly limiting during the later regeneration phases.

5.3. The results in context

This study successfully achieved its objectives of analyzing the impacts of several key gap characteristics on natural vegetation and seedling regeneration. The results of this study are generally in line with the hypotheses and reflect the findings of existing relevant and overlapping research. No significant issues were encountered in the data collection or the data analysis phases. Therefore, the data produced by this study are believed to be representative of the phenomena which it sought to study. Nevertheless, the results and the models have inherent limitations which will be discussed in the following sections.

5.3.1. The modeling approach

Since the data displayed largely unknown non-linear relationships between the mean number of seedlings and explanatory variables, this study chose to implement non-parametric techniques to uncover these relationships. The benefit of using generalized additive models (GAMs) is that in being very flexible, they can more effectively uncover the unknown, unique and sometimes complex non-linear relationships between variables. In this study, the GAMs did just that; they greatly facilitated the estimation of the unique response curves for the wide array of covariates measured.

On the other hand, it is possible that the flexibility of the GAMs overestimated the complexity of the relationships. In some cases, a simpler curve (e.g., monotonic, parametric) could have proven more adequate. Relatively wide confidence intervals in a GAM curve

might be indicative of such a situation. Accordingly, with this data a simpler curve might have been more appropriate to describe the effect of herbs and decayed/young stumps or logs on the densities of Norway spruce and birch seedlings, respectively.

Nevertheless, GAMs were a very useful tool for helping to uncover the more complex elements of the relationships between variables. Since the purpose of modeling in this study was to describe the relationships between the measured variables, the GAM approach was generally quite adequate. Furthermore, care was taken during the modeling process to ensure that the curves predicted by the GAMs were reasonable in the context of existing literature. However, in order produce more robust models which could be used as predictive tools, further modeling-based analyses would be recommended. For example, based on the estimated GAM curves produced here, unique parametric (and likely non-linear) response functions could be developed for each of the covariates. Then, these functions would be combined to tentatively build a parametric model explaining the density of seedlings. Next, like the method described in Section 3.3.4 for testing the significance of linear reference models, a GAM could be fit to explain the residuals of this parametric model as a function of the same covariates. Depending on the resulting GAM summary, it may be necessary to repeat this process until results suggest that the data have been adequately characterized by the parametric functions.

5.3.2. Seed production and climate

In this study, the timing of tree seed production as well as the abundance of seeds produced was not directly addressed. Since seedling regeneration is as much about seed production as it is about seedling establishment and survival, the characteristics included in the models cannot fully explain the magnitudes of the seedlings observed across the gaps. For Norway spruce, cone production varies significantly between years (Jonsson and Hofgaard 2011), as well as between similar trees within a forest stand (Juntunen and Neuvonen 2006). For adaptive reasons, abundant Norway spruce cone production very seldom occurs two years in a row (Pukkala et al. 2010), and sometimes only occur once in 4 years (Broome et al. 2007). For birch species, the quantity of seeds also varies significantly over time, with abundant seed crops occurring only every 2 to 3 years in Northern Europe (Sarvas 1948, Koski and Tallqvist 1978). Therefore, since this study was conducted only within 5 growing seasons of gap creation, the variability in seed production likely had a significant impact on these results.

Since climatic conditions and between-year climate variability plays a central role in determining the seed production for both Norway spruce (Lindgren et al. 1977, Leikola et al. 1982, Pukkala 1987, Nikkanen and Ruotsalainen 2000) and birch species (Sarvas 1948, Koski and Tallqvist 1978), perhaps the models could have been calibrated by an index which reflects the estimated effect of climate on seed production. The index could be based on existing research, for example on models predicting seedling abundance according to recorded climatic variables. For example, such a model was recently created for Norway spruce (Pukkala et al. 2010). Climate also affects the establishment, survival and growth dynamics of Norway spruce (Repo 1992, Lundmark et al. 1998, Hannerz 1999, Selås et al. 2002) and birch seedlings (Vaartaja 1952, Black and Wareing 1954, Black and Wareing 1955, Vanhatalo et al. 1996). Therefore, including climatic variables in the models could have also improved on their ability to accurately assess the factors responsible for the patterns of seedling regeneration, as well as their respective magnitudes.

5.3.3. Temporal variation

The decades after gap creation are characterised by a series of localized environmental changes, which create cumulative dynamic interactions among the various abiotic (e.g., microsites) and biotic (e.g., microbes, fungi, vegetation, seedlings) components. For this reason, the microsites observed, the extent of the influence of the forest edge, as well as the distribution of vegetation species across the gap environment will themselves be subject to change as the gap ages. Therefore, the dynamics of seedling regeneration will not only be a function of seedling emergence and survival but also a function of how and where these subsequent changes will occur.

Firstly, the effect of the forest edge as well as the extent of the zone most influenced by the edge change considerably over time (Matlack 1994, Harper and Macdonald 2002, Harper et al. 2005). Also, as the inner gap region regenerates, the edge zone itself becomes less defined and therefore its influence diminishes (Fahey and Puettmann 2008). Therefore, the spatial patterns of vegetation and seedling abundance relative to the edge are likely to change significantly over time. Moreover, the extent of the below-ground competition from edge trees is likely to increase over time as their roots slowly expand into the inner gap region (Taskinen et al. 2003), further affecting the edge zone dynamics.

In terms of vegetation and tree species, researchers generally agree on one conclusion concerning forest gaps: gap interiors generally promote a greater diversity and abundance of species than the residual undisturbed forest stand (Kuuluvainen 1994, Narukawa and Yamamoto 2001, Schumann et al. 2003, Fahey and Puettmann 2008, Kirchner et al. 2011, Kern et al. 2014). However, the composition of this vegetation and seedling community will not remain stable over time, and diversity tends to decrease with increasing gap age (Halpern and Spies 1995, Franklin et al. 2002). The main drivers of these dynamics are the species' ability to disperse, the availability of suitable microsites and later their ability to compete with other vegetation (Dovciak et al. 2003, Kirchner et al. 2011).

Shortly after gap creation, it is the early pioneer species (species which can quickly disperse and establish themselves) which tend to increase in coverage. Most notably, grasses and sedges are of the first to colonize gaps since they can disperse very easily through their wind-borne seeds (Whitmore 1978, Leder 1992, Goldblum 1997, Yamamoto 2000, Hartig and Lemke 2002, Holeksa 2003, Kirchner et al. 2011). Also, herbs tend to increase in cover and spread fairly rapidly after harvest, and then slowly continue to increase in cover with time (Kooijman et al. 2000, Diaci 2002, Man et al. 2009, Valkonen et al. 2011, Kirchner et al. 2011). However, as gap age increases, the species which dominate the gap environment at first will typically decline as succession proceeds (Halpern and Spies 1995, Schumann et al. 2003). On the other hand, shrubs and dwarf shrubs disperse clonally, and reportedly decrease in cover after harvest (Kooijman et al. 2000, Jalonen and Vanha-Majamaa 2001, Harper and Macdonald 2002, Kirchner et al. 2011). However, over time they can grow into dense patches connected by a network of thick rhizomes, making it possible for them to effectively compete with other vegetation and expand their coverage in some areas (Bråkenhielm and Persson 1980, Hautala et al. 2001). These are but a few examples of the changes in vegetation coverage which occur over time.

Microsites conditions also evolve with time after gap creation, processes which continuously alter the suitability of microsites for vegetation and seedling regeneration (Kathke and Bruelheide 2010b, Kirchner et al. 2011). For example, logs and stumps decay with increasing gap age, accelerated by warmer temperatures and increased biological activity. As stumps and logs decay, they are first colonized by mosses and lichens, later by dwarf shrubs, and lastly by herbs and grasses (Hofgaard 1993, Zielonka and Piątek 2004, Kirchner et al. 2011). In conclusion, the combined effects of these changes in vegetation and microsite conditions

over time mean that the results of this study are extremely temporally limited, and only truly describe the patterns and dynamics of early regeneration in the gaps.

5.3.4. Seed-seedling conflict

During recent decades, research has revealed that the conditions favorable for seedling emergence and germination often do not directly correlate with the conditions necessary for the successful long-term regeneration of seedlings; this seed-seedling conflict was first described by Schupp (1995). For these reasons, even once established, spruce and birch seedlings will often experience high levels of mortality (Leemans 1991, Hofgaard 1993, Huth and Wagner 2006). One mechanism which can explain this high level of mortality is self-thinning, which occurs where overly high densities of seedlings have established on very favorable microsites (Runkle 1998). Consequently, areas which have been described to support high numbers of seedlings in this study will not necessarily support the most successful regeneration over time.

For example, although stumps and logs are known to support higher densities of young seedlings (as discussed in Section 1.2.2), these microsites are also linked to higher than normal inter-seedling competition (Kuuluvainen and Kalmari 2003, Vodde et al. 2010), as well as greater competition from other vegetation (Harmon and Franklin 1989, Zielonka 2006). Consequently, stumps and logs are also associated with slow seedling growth rates and high seedling mortality in the long-run (Szewczyk and Szwagrzyk 1996, Kupferschmid and Bugmann 2005, Kathke and Bruelheide 2010b). Therefore, although the models in this study revealed that stumps and logs were important microsites for young birch seedlings, perhaps the patterns of successful long-term seedling regeneration will prove otherwise.

On the other hand, covered stones are generally poorer establishment microsites for young seedlings, possibly due to the greater drought risk caused by thick moss layers (Hornberg et al. 1997, Zielonka and Niklasson 2001) or to greater levels of competition from dwarf shrubs (Kirchner et al. 2011). However, since covered stones host lower levels of inter-seedling competition, seedling survival has often been superior there than on other microsites (Kuuluvainen and Kalmari 2003, Kathke and Bruelheide 2010b). Therefore, perhaps the importance of covered stones in the long-term spruce (and birch) seedling regeneration is underrepresented in the results of this study.

Depressions have generally been found to host greater densities of seedlings than do other topographies (as discussed in Section 1.2.3), findings which are supported by results on spruce seedling density in this study. However, depressions can be highly unstable sites for seedling establishment (Vodde et al. 2011). Greater risks of seedling inundation, damage from litter accumulation, as well as higher inter-seedling competition in these topographies all lead to higher levels of seedling mortality (Hanssen 2003, Ilisson et al. 2007, Grenfell et al. 2011). Consequently, the importance of depressions for the long-term regeneration potential of Norway spruce seedlings may be overestimated by these results.

Lastly, the spatial patterns of seedling establishment in the gaps is likely going to change over time as a result of the combined effects of optimal light conditions and competition dynamics. This will probably be of greatest importance for birch seedlings. Research has shown that although generally shade intolerant, birch seedlings can successfully establish in shaded environments if suitable levels of nutrients and water are available (Perala and Alm 1990b). Accordingly, several studies found adequate young birch seedling establishment in small shaded gaps or under shelterwood systems (Nilsson et al. 2002, Karlsson and Nilsson 2005, Huth and Wagner 2006). These studies support the patterns observed in this study, where high densities of young birch seedlings were observed in the shadier southern and near-edge gap positions. However, studies on long-term regeneration patterns of birch show that seedlings which established in shadier areas tended to experience slower growth and higher rates of mortality (Perala and Alm 1990a, Huth and Wagner 2006, Friesen and Michaels 2010).

Conversely, in full-sun conditions, Huth and Wagner (2006) observed fairly low densities of young birch seedlings (~2–4 years old), attributed to greater levels of competition from grasses in these areas. However, these birch seedlings had greater rates of survival and growth than seedlings in other gap positions in the long-run. Valkonen et al. (2011) confirmed these trends in their study on natural regeneration in forest patches 10 years after harvest, where they found greater birch seedling densities in patch centers compared to inner patch edges and residual forest zones.

To summarize, these findings indicate that although competition pressures may largely dictate the patterns of early birch seedling establishment, their long-term regeneration success may more greatly reflect the patterns of light availability. As results from Valkonen et al.

(2011) suggest, this seed-seedling conflict may become evident even within a relatively short period of time (~10 years) after seedling establishment. Consequently, although southern and edge gap positions currently show larger birch seedling densities, it is possible that the seedlings which established in the central (or northern) gap positions will survive and grow better over time.

6. CONCLUSIONS

The purpose of the study was to record the patterns of early Norway spruce and birch seedling regeneration across small- to medium-sized boreal forest gaps, and to explain these patterns according to several of the most significant factors which affect them. This study successfully included several of the factors which are known to most affect early seedling regeneration success, namely competition with vegetation, microsite conditions and position within the gap. Since the early stages of natural regeneration play a crucial role in determining its long-term success (Kozlowski 2002), the results of this study support a deeper understanding of the factors and spatial characteristics which govern seedling regeneration across boreal forest gaps.

As a result of seed-seedling conflicts as well as the temporally dynamic nature of vegetation and seedling regeneration following harvesting, the models created are not predictive tools used to quantify the regeneration success of seedlings across gap environments. Instead, the models are tools which can help to better describe the interactions and spatial patterns which affect early seedling regeneration in gaps. In the context of disturbance emulation forestry, these results can help effectively guide forest planners and management practitioners in developing strategies designed to promote the conditions which support the early regeneration success of Norway spruce and birch seedlings, and to limit the factors which hinder it.

The models revealed that the factors which most significantly affect the regeneration of Norway spruce seedlings are distance from the gap edge, basal area, topography and the percent cover of shrubs, dwarf shrubs, herbs and grasses. The percent cover of duff was also significant for older seedlings. Consequently, the results of this study suggest that if Norway spruce regeneration is required, it may be wise to intentionally create depressions and mounds through site preparation techniques. In addition, care should be taken during forest harvesting not to disturb or remove existing microsites such as covered stones and duff, which are important for the early regeneration of Norway spruce seedlings.

The models revealed that the factors which most significantly affect the regeneration of birch seedlings are distance from the gap edge, basal area, cardinal position in the gap and the percent cover of grasses, stumps and decayed stumps or logs. The percent cover of dwarf

shrubs was also important for younger seedlings. Therefore, if the natural regeneration of birch species is required, it would be favorable to leave new stumps and logs in the gap during harvesting operations, and to not remove or disturb the existing stumps and logs.

If mechanical vegetation management practices are included in the array of tools at the disposal of forest managers, it could potentially enhance the regeneration potential of both Norway spruce and birch seedling regeneration in gaps. Vegetation management should focus on shrubs, dwarf shrubs and grasses, since these were the species which seemed to most negatively affect the natural regeneration of both species.

These results, along with previous research, suggest that natural regeneration within the 0–15m zone may be adequate in gaps, at least initially. However, the region beyond 15m from the edge towards gap center has experienced limited seedling establishment during the first years after gap creation, largely owing to the high levels of competition with understory vegetation. Therefore, vegetation management should focus on this region (and somewhat closer to the gap edge in northern gap positions) in order to promote the long-term regeneration success of Norway spruce and birch seedlings.

If no vegetation management is possible, gap diameters of ≤30–40m could potentially support the highest overall density of established seedlings. However, as a consequence of seed-seedling conflicts discussed in Section 5.3.4, larger gap diameters may be required to support adequate growth of birch seedlings in the long-run. Nevertheless, the results of this study suggest adequate potential for long-term natural regeneration in similar small- to medium-sized forest gaps.

Continued research in the context of the DISTDYN project will allow these dynamics and trends to be monitored as the regeneration process continues to evolve. By including vegetation, microsites, topography and within-gap position in the research, studies under the DISTDYN project will greatly contribute to a more thorough understanding of the long-term dynamics of natural regeneration in the context of disturbance emulation forestry, as well as more broadly contribute to the regeneration science literature. Since forest canopy gaps play a central role in the regeneration dynamics typical of natural forests in Fennoscandia (Hytteborn et al. 1987, Leemans 1990, Leemans 1991, Liu and Hytteborn 1991), this study specifically addresses questions relevant to the future of disturbance emulation forestry in

these regions. Finally, as one of the first steps in a longer research journey in these forests, the results of this study will continue to help researchers uncover both the broader and the finer-scale details which govern the patterns of natural regeneration across forest gaps in boreal Fennoscandia.

REFERENCES

Ackzell, L. 1994. Forest regeneration by nature and man. Department of forest genetics and plant physiology: Swedish University of Agricultural Sciences, Umeå.

Ammer, C. & Wagner, S. 2002. Problems and options in modelling fine-root biomass of single mature Norway spruce trees at given points from stand data. Canadian Journal of Forest Research 32: 581-590.

Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9: 593-602.

Asselin, H., Fortin, M. J. & Bergeron, Y. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. Forest Ecology and Management 140: 29-37.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Aukema, J. E. & Carey, A. B. 2008. Effects of variable-density thinning on understory diversity and heterogeneity in young Douglas-fir forests. USDA Forest Service - Research Paper PNW-RP-575: 1-20.

Auvinen, A. P., Hildén, M., Toivonen, H., Primmer, E., Niemelä, J., Aapala, K., Bäck, S., Härmä, P., Ikävalko, J., Järvenpää, E., Kaipiainen, H., Korhonen, K. T., Kumela, H., Kärkkäinen, L., Lankoski, J., Laukkanen, M., Mannerkoski, I., Nuutinen, T., Nöjd, A., Punttila, P., Salminen, O., Söderman, G., Törmä, M. & Virkkala, R. 2007. Evaluation of the Finnish National Biodiversity Action Plan 1997-2005. Monographs of the Boreal Environment Research 29: 1-55.

Battles, J. J. & Fahey, T. J. 2000. Gap dynamics following forest decline: A case study of red spruce forests. Ecological Applications 10: 760-774.

Bazzaz, F. A. & Wayne, P. M. 1994. Coping with environmental heterogeneity: The physiological ecology of tree seedling regeneration across the gap-understory continuum. In: Caldwell, M. M. & Pearcy, R. W. (eds.). Exploitation of Environmental Heterogeneity by Plants. San Diego: Academic Press, pp. 349-390.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65: 1406-1419.

Béland, M. & Chicoine, B. 2013. Tolerant hardwood natural regeneration 15 years after various silvicultural treatments on an industrial freehold of northwestern New Brunswick. Forestry Chronicle 89: 512-524.

Bell, F. W., Ter-Mikaelian, M. T. & Wagner, R. G. 2000. Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. Canadian Journal of Forest Research 30: 790-800.

Bergeron, Y., Harvey, B., Leduc, A. & Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. The Forestry Chronicle 75: 49-54.

Bergeron, Y., Leduc, A., Harvey, B. D. & Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36: 81-95.

Bergstedt, J. & Milberg, P. 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. Forest Ecology and Management 154: 105-115.

Betz, H. 1998. Untersuchungen zur Ausbreitungsökologie des Wolligen Reitgrases (Calamagrostis villosa (Chaix.) J.F.Gmel.). Bayreuther Forum Ökologie 59: 1-207.

Biswas, S. R. & Mallik, A. U. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91: 28-35.

Bjor, K. 1971. Forest meteorological, soil climatological and germination investigations. Meddelelser fra Det norske Skogforsøksvesen 28: 429-526.

Black, M. & Wareing, P. F. 1954. Photoperiodic control of germination in seed of birch (Betula pubescens Ehrh.). Nature 174: 705-706.

Black, M. & Wareing, P. F. 1955. Growth studies in woody species VII. Photoperiodic control of germination in Betula pubescens Ehrh. Physiologia Plantarum 8: 300-316.

Bradshaw, F. 1992. Quantifying edge effect and patch size for multiple-use silviculture—a discussion paper. Forest Ecology and Management 48: 249-264.

Braithwaite, N. T. & Mallik, A. U. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. Journal of Applied Ecology 49: 192-201.

Bråkenhielm, S. & Persson, H. 1980. Vegetation dynamics in developing Scots pine stands in central Sweden. Ecol.Bull. 32: 139-152.

Brang, P. 1996. Experimentelle Untersuchungen zur Ansamungsökologie der Fichte im zwischenalpinen Gebirgswald. Beih.Schweiz.Z.Forstwes 77: 1-375.

Bratton, S. P. 1994. Logging and fragmentation of broadleaved deciduous forests: Are we asking the right ecological questions? Conservation Biology 8: 295-297.

Brockway, D. G. & Outcalt, K. W. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. Forest Ecology and Management 106: 125-139.

Broome, A., Hendry, S. & Peace, A. 2007. Annual and spatial variation in coning shown by the Forest Condition Monitoring programme data for Norway spruce, Sitka spruce and Scots pine in Britain. Forestry 80: 17-28.

Burton, P. J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. Silva Fennica 36: 329-352.

Busing, R. T. 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. Vegetatio 115: 19-27.

Cadenasso, M. L., Traynor, M. M. & Pickett, S. T. A. 1997. Functional location of forest edges: Gradients of multiple physical factors. Canadian Journal of Forest Research 27: 774-782.

Cajander, A. K. 1909. Über Waldtypen. Acta Forestalia Fennica 1: 1-175.

Caldwell, J. M., Sucoff, E. I. & Dixon, R. K. 1995. Grass interfernece limits resource availability and reduces growth of juvenile red pine in the field. New Forests 10: 1-15.

Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69: 1634-1638.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A. & White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20: 620-631.

Carlton, G. C. & Bazzaz, F. A. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecological Monographs 68: 99-120.

Caron, M. N., Kneeshaw, D. D., Grandpré, L. D., Kauhanen, H. & Kuuluvainen, T. 2009. Canopy gap characteristics and disturbance dynamics in old-growth Picea abies stands in northern fennoscandia: Is the forest in quasi-equilibrium? Annales Botanici Fennici 46: 251-262.

Chazdon, R. L. & Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72: 553-564.

Chen, J., Franklin, J. F. & Spies, T. A. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology 63: 219-237.

Chen, J., Franklin, J. F. & Spies, T. A. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecological Applications 5: 74-86.

Clarke, G. C. 1992. The natural regeneration of spruce. Scottish Forestry 46: 107-129.

Coates, K. D. 2000. Conifer seedling response to northern temperate forest gaps. Forest Ecology and Management 127: 249-269.

Coates, K. D. & Burton, P. J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. Forest Ecology and Management 99: 337-354.

Coll, L., Balandier, P. & Picon-Cochard, C. 2004. Morphological and physiological responses of beech (Fagus sylvatica) seedlings to grass-induced belowground competition. Tree physiology 24: 45-54.

Coomes, D. A., Allen, R. B., Bentley, W. A., Burrows, L. E., Canham, C. D., Fagan, L., Forsyth, D. M., Gaxiola-Alcantar, A., Parfitt, R. L., Ruscoe, W. A., Wardle, D. A., Wilson, D. J. & Wright, E. F. 2005. The hare, the tortoise and the crocodile: The ecology of angiosperm dominance, conifer persistence and fern filtering. Journal of Ecology 93: 918-935.

Cornett, M. W., Puettmann, K. J. & Relch, P. B. 1998. Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. Canadian Journal of Forest Research 28: 196-205.

Dai, X. 1996. Influence of light conditions in canopy gaps on forest regeneration: A new gap light index and its application in a boreal forest in east-central Sweden. Forest Ecology and Management 84: 187-197.

Davis, M. A., Wrage, K. J., Reich, P. B., Tjoelker, M. G., Schaeffer, T. & Muermann, C. 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecology 145: 341-350.

De Chantal, M., Leinonen, K., Kuuluvainen, T. & Cescatti, A. 2003. Early response of Pinus sylvestris and Picea abies seedlings to an experimental canopy gap in a boreal spruce forest. Forest Ecology and Management 176: 321-336.

den Ouden, J. 2000. The role of bracken (Pteridium aquilinum) in forest dynamics. Wageningen University, Wageningen.

Diaci, J. & Boncina, A. 2005. Regeneration in experimental gaps of subalpine Picea abies forest in the Slovenian Alps. European journal of forest research 124: 29-36.

Diaci, J. 2002. Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. Forest Ecology and Management 161: 27-38.

Dolling, A., Zackrisson, O. & Nilsson, M. C. 1994. Seasonal variation in phytotoxicity of bracken (Pteridium aquilinum L. Kuhn). Journal of Chemical Ecology 20: 3163-3172.

Dolling, A. H. U. 1996. Interference of bracken (Pteridium aquilinum L. Kuhn) with Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies L. Karst.) seedling establishment. Forest Ecology and Management 88: 227-235.

Domke, G. M., Caspersen, J. P. & Jones, T. A. 2007. Light attenuation following selection harvesting in northern hardwood forests. Forest Ecology and Management 239: 182-190.

Dovciak, M., Reich, P. B. & Frelich, L. E. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. Canadian Journal of Forest Research 33: 1892-1904.

Dragulescu, A. A. 2014. xlsx: Read, write, format Excel 2007 and Excel 97/2000/XP/2003 files. R package version 0.5.7.

Drever, C. R., Peterson, G., Messier, C., Bergeron, Y. & Flannigan, M. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36: 2285-2299.

Drobyshev, I. V. 2001. Effect of natural disturbances on the abundance of Norway spruce (Picea abies L. Karst.) regeneration in nemoral forests of the southern boreal zone. Forest Ecology and Management 140: 151-161.

Du Rietz, G. E., Nannfeldt, J. A. & Nordhagen, R. 1952. Våre ville planter. Moser. Lav. Sopp. Bind VII. Oslo: Forlagt av Johan Grundt Tanum. 314 p.

Duchaufour, P. 1982. Pedology: Pedogenesis and Classification. London: Allen and Unwin. 448 p.

Dumas, Y. 2002. An overview of bracken. Revue Forestiere Francaise 54: 357-374.

Eissenstat, D. M. & Newman, E. I. 1990. Seedling establishment near large plants: effects of vesicular- arbuscular mycorrhizas on the intensity of plant competition. Functional Ecology 4: 95-99.

Engelmark, O. & Hytteborn, H. 1999. Coniferous forests. Acta Phytogeographica Suecica 84: 55-74.

Eriksson, O. & Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91: 360-364.

Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16-47.

Fahey, R. T. & Puettmann, K. J. 2008. Patterns in spatial extent of gap influence on understory plant communities. Forest Ecology and Management 255: 2801-2810.

Fanta, J. & Kobus, A. 1995. Restoration of forest ecosystems in Krokonose Mountains: Preliminary results of an inventory study. Management of Forest Damaged by Air Pollution. Brno: IUFRO, pp. 97-102.

Fleming, R. L. & Mossa, D. S. 1994. Direct seeding of black spruce in northwestern Ontario: Seedbed relationships. Forestry Chronicle 70: 151-158.

Flinn, K. M. & Vellend, M. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3: 243-250.

Forman, R. T. T. 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge, UK: Cambridge University Press.

Fox, J. & Weisberg, S. 2011. An {R} Companion to Applied Regression. Second Edition edition. Sage: Thousand Oaks CA.

Franklin, J. F., Spies, T. A., Pelt, R. V., Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K. & Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155: 399-423.

Fraver, S., Jonsson, B. G., Jönsson, M. & Esseen, P. A. 2008. Demographics and disturbance history of a boreal old-growth Picea abies forest. Journal of Vegetation Science 19: 789-798.

Friesen, C. & Michaels, N. 2010, Effects of Incorporating Gaps into Commercial Thinning Prescriptions: Best Available Science. Central Cascades Adaptive Management Partnership (CCAMP).

Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K. & Standovár, T. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. Plant Ecology 183: 133-145.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Canadian Journal of Forest Research 27: 139-147.

Gallet, C. 1994. Allelopathic potential in bilberry-spruce forests: influence of phenolic compounds on spruce seedlings. Journal of Chemical Ecology 20: 1009-1024.

Gallet, C. & Lebreton, P. 1995. Evolution of phenolic patterns in plants and associated litters and humus of a mountain forest ecosystem. Soil Biology and Biochemistry 27: 157-165.

Gärdenfors, U. 2005. The 2005 red list of Swedish species. Uppsala: Swedish Species Information Centre, SLU.

Gastaldello, P. 2005. Remise en production des bétulaies jaunes résineuses dégradées: Étude du succès d'installation de la régénération et des variations biophysiques et physionomiques à l'intérieur du lit de germination. Mémoire maîtrise. Université Laval.

Gastaldello, P., Ruel, J. & Paré, D. 2007. Micro-variations in yellow birch (Betula alleghaniensis) growth conditions after patch scarification. Forest Ecology and Management 238: 244-248.

Gauthier, S., Vaillancourt, M., Leduc, A., DeGarndpre, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. 2009. Ecosystem management in the boreal forest. Québec, QC: Les Presses de l'Université du Québec.

George, L. O. & Bazzaz, F. A. 1999a. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. Ecology 80: 833-845.

George, L. O. & Bazzaz, F. A. 1999b. The fern understory as an ecological filter: Growth and survival of canopy-tree seedlings. Ecology 80: 846-856.

George, L. O. & Bazzaz, F. A. 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gilliam, F. S. & Roberts, M. R. (eds.). The Herbaceous Layer in Forests of Eastern North America. New York: Oxford University Press, pp. 265-282.

Gilliam, F. S. & Roberts, M. R. (eds.) 2003. The Herbaceous Layer in Forests of Eastern North America. New York: Oxford University Press.

Gimingham, C. H. 1984. Ecological aspects of birch. Proceedings of the Royal Society of Edinburgh Section B, Biological Sciences 85: 65-72.

Goldberg, D. E. 1990. Components of resource competition in plant communities. In: Grace, J. & Tilman, D. (eds.). Perspectives on Plant Competition. San Diego: Academic Press, pp. 27-49.

Goldblum, D. 1997. The effects of treef all gaps on understory vegetation in New York State. Journal of Vegetation Science 8: 125-132.

Gray, A. N. & Spies, T. A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology 84: 635-645.

Grenfell, R., Aakala, T. & Kuuluvainen, T. 2011. Microsite occupancy and the spatial structure of understorey regeneration in three late-successional Norway spruce forests in Northern Europe. Silva Fennica 45: 1093-1110.

Gromtsev, A. 2002. Natural disturbance dynamics in the boreal forests of European Russia: A review. Silva Fennica 36 (1): 41-55.

Groot, A. & Adams, M. J. 1994. Direct seeding black spruce on peatlands: Fifth-year results. Forestry Chronicle 70: 585-592.

Grushecky, S. T. & Ann Fajvan, M. 1999. Comparison of hardwood stand structure after partial harvesting using intensive canopy maps and geostatistical techniques. Forest Ecology and Management 114: 421-432.

Gustafsson, L., Kouki, J. & Sverdrup-Thygeson, A. 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: A review of ecological consequences. Scandinavian Journal of Forest Research 25: 295-308.

Hagner, S. 1962. Natural regeneration under shelterwood stands. Meddelanden Från Statens Skogsforskningsinstitut 52.

Halpern, C. B., McKenzie, D., Evans, S. A. & Maguire, D. A. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications 15: 175-195.

Halpern, C. B. & Spies, T. A. 1995. Plant species diversity in natural and managed forests of the Pacific northwest. Ecological Applications 5: 913-934.

Hannerz, M. 1999. Evaluation of temperature models for predicting bud burst in Norway spruce. Canadian Journal of Forest Research 29: 9-19.

Hansen, A. J., Garman, S. L., Lee, P. & Horvath, E. 1993. Do edge effects influence tree growth rates in Douglas-fir plantations? Northwest Science 67: 112-116.

Hanski, I. 2000. Extinction debt and species credit in boreal forests: Modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37: 271-280.

Hanssen, K. H. 1996. Natural regeneration of spruce (Picea abies) on clear cuttings. Preliminary results from a field study in south-east Norway. In: Skovsgaard, J. P. & Johannsen, V. K. (eds.). Modelling Regeneration Success and Early Growth of Forest Stands. Proceedings from the IUFRO Conference held in Copenhagen, 10-13 June. , pp. 351-362.

Hanssen, K. H. 2002. Effects of seedbed substrates on regeneration of Picea abies from seeds. Scandinavian Journal of Forest Research 17: 511-521.

Hanssen, K. H. 2003. Natural regeneration of Picea abies on small clear-cuts in SE Norway. Forest Ecology and Management 180: 199-213.

Hanssen, K. H., Granhus, A., Braekke, F. H. & Haveraaen, O. 2003. Performance of sown and naturally regenerated Picea abies seedlings under different scarification and harvesting regimens. Scandinavian Journal of Forest Research 18: 351-361.

Harmon, M. E. & Franklin, J. F. 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70: 48-59.

Harper, K. A., Lesieur, D., Bergeron, Y. & Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Canadian Journal of Forest Research 34: 289-302.

Harper, K. A. & Macdonald, S. E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. Journal of Vegetation Science 13: 535-546.

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S. & Esseen, P. A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19: 768-782.

Hartig, M. & Lemke, C. 2002. Birken-Schneesaat: Eine in Vergessenheit geratene Walderneuerungsmethode. Allgemeine Forstzeitschrift - Der Wald (4): 170–173.

Hautala, H., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2011. Effects of retention felling on epixylic species in boreal spruce forests in Southern Finland. Restoration Ecology 19: 418-429.

Hautala, H., Tolvanen, A. & Nuortila, C. 2001. Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. Journal of Vegetation Science 12: 503-510.

Haveri, B. A. & Carey, A. B. 2000. Forest management strategy, spatial heterogeneity, and winter birds in Washington. Wildlife Society Bulletin 28: 643-652.

Heikinheimo, O. 1932. Metsapuiden siementamiskyvysta. Refererat: Über die Besanmungsfahigkeit der Waldbaume [Seed production capacity of forest trees]. Communicationes Instituti Forestalis Fenniae 17: 55.

Heikinheimo, O. 1937. Metsäpuiden siementämiskyvystä II. Deutsches referat: Über die besamungsfähigkeit der waldbäume II. Commun. Inst. For. Fenn. 24: 1-67.

Hendrickson, O. Q. 1991. Abundance and activity of N_2-fixing bacteria in decaying wood. Canadian Journal of Forest Research 21: 1299-1304.

Hertz, M. 1932. Über die Bedeutung der Untervegetation für die Verjüngung der Fichte auf den südfinnischen Heideböden [The importance of understory vegetation on spruce regeneration in southern Finnish heathlands]. Communicationes Instituti Forestalis Fenniae 17: 206.

Hesselman, H. 1938. Fortsatta studier över tallens och granens fröspridning samt kalhyggets besåning. Meddelanden från Statens Skogförsöksanstalt 31: 1-64.

Hill, S. B., Mallik, A. U. & Chen, H. Y. H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Canadian Journal of Forest Research 35: 1942-1951.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin Picea abies forest in northern Sweden. Journal of Vegetation Science 4: 601-608.

Holeksa, J. 2003. Relationship between field-layer vegetation and canopy openings in a Carpathian subalpine spruce forest. Plant Ecology 168: 57-67.

Hornberg, G., Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research 27: 1015-1023.

Huggard, D. J. & Vyse, A. 2002a. Comparing clearcutting and alternatives in a high-elevation forest: early results from Sicamous Creek, Extension Note 63. British Columbia Ministry of Forests Forest Science Program.

Huggard, D. J. & Vyse, A. 2002b. Edge Effects in High-elevation Forests at Sicamous Creek, Extension Note 62. British Columbia Ministry of Forests Forest Science Program.

Hughes, J. W. & Bechtel, D. A. 1997. Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. Canadian Journal of Forest Research 27: 2088-2096.

Humphrey, J. W. & Swaine, M. D. 1997. Factors affecting the natural regeneration of Quercus in Scottish oakwoods. I. Competition from Pteridium aquilinum. Journal of Applied Ecology 34: 577-584.

Hunter, J., M.L. 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press.

Hunziker, U. & Brang, P. 2005. Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. Forest Ecology and Management 210: 67-79.

Huston, M. & Smith, T. 1987. Plant succession: life history and competition. American Naturalist 130: 168-198.

Huth, F. & Wagner, S. 2006. Gap structure and establishment of Silver birch regeneration (Betula pendula Roth.) in Norway spruce stands (Picea abies L. Karst.). Forest Ecology and Management 229: 314-324.

Hytönen, J. & Jylhä, P. 2005. Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to Betula pendula planted on former agricultural land. Silva Fennica 39: 365-380.

Hytteborn, H. & Packham, J. R. 1987. Decay rate of Picea abies logs and the storm gap theory: a re- examination of Sernander plot III, Fiby urskog, central Sweden. Arboricultural Journal 11: 299-311.

Hytteborn, H., Packham, J. R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibäcken, northern Sweden. Vegetatio 72: 3-19.

Iijima, H. & Shibuya, M. 2010. Evaluation of suitable conditions for natural regeneration of Picea jezoensis on fallen logs. Journal of Forest Research 15: 46-54.

Ilisson, T., Köster, K., Vodde, F. & Jõgiste, K. 2007. Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecology and Management 250: 17-24.

Itô, H. & Hino, T. 2007. Dwarf bamboo as an ecological filter for forest regeneration. Ecological Research 22: 706-711.

Jäderlund, A., Norberg, G., Zackrisson, O., Dahlberg, A., Teketay, D., Dolling, A. & Nilsson, M. C. 1998. Control of bilberry vegetation by steam treatment - Effects on seeded Scots pine and associated mycorrhizal fungi. Forest Ecology and Management 108: 275-285.

Jäderlund, A., Zackrisson, O., Dahlberg, A. & Nilsson, M. C. 1997. Interference of Vaccinium myrtillus on establishment, growth, and nutrition of Picea abies seedlings in a northern boreal site. Canadian Journal of Forest Research 27: 2017-2025.

Jäderlund, A., Zackrisson, O. & Nilsson, M. C. 1996. Effects of bilberry (Vaccinium myrtillus L.) litter on seed germination and early seedling growth of four boreal tree species. Journal of Chemical Ecology 22: 973-986.

Jalonen, J. & Vanha-Majamaa, I. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. Forest Ecology and Management 146: 25-34.

Jeglum, J. K. & Kennington, D. J. (eds.) 1993. Strip Clearcutting in Black Spruce: A Guide for the Practicing Forester. Sault Ste Marie, Ontario: Great Lakes Forestry Centre.

Jonsell, B. (ed.) 2000. Flora Nordica. Volume 1. Lycopodiaceae to Polygonaceae. Stockholm, Sweden: The Bergius Foundation, the Royal Swedish Academy of Sciences. 344 p.

Jonsson, B. G. & Hofgaard, A. 2011. The structure and regeneration of high-altitude Norway spruce forests: A review of Arnborg (1942, 1943). Scandinavian Journal of Forest Research 26: 17-24.

Juntunen, V. & Neuvonen, S. 2006. Natural regeneration of Scots pine and Norway spruce close to the timberline in northern Finland. Silva Fennica 40: 443-458.

Jurgensen, M. F., Larsen, M. J., Graham, R. T. & Harvey, A. E. 1987. Nitrogen fixation in woody residue of northern Rocky Mountain conifer forests. Canadian Journal of Forest Research 17: 1283-1288.

Karlsson, C. & Örlander, G. 2000. Soil scarification shortly before a rich seed fall improves seedling establishment in seed tree stands of Pinus sylvestris. Scandinavian Journal of Forest Research 15: 256-266.

Karlsson, M. 2001. Natural regeneration of broadleaved tree species in Southern Sweden. Southern Swedish Forest Research Centre, SLU.

Karlsson, M. & Nilsson, U. 2005. The effects of scarification and shelterwood treatments on naturally regenerated seedlings in southern Sweden. Forest Ecology and Management 205: 183-197.

Karlsson, M., Nilsson, U. & Örlander, G. 2002. Natural regeneration in clear-cuts: Effects of scarification, slash removal and clear-cut age. Scandinavian Journal of Forest Research 17: 131-138.

Kathke, S. & Bruelheide, H. 2010a. Gap dynamics in a near-natural spruce forest at Mt. Brocken, Germany. Forest Ecology and Management 259: 624-632.

Kathke, S. & Bruelheide, H. 2010b. Interaction of gap age and microsite type for the regeneration of Picea abies. Forest Ecology and Management 257: 1070-1077.

Kauppi, A., Rinne, P. & Ferm, A. 1987. Initiation, structure and sprouting of dormant basal buds in Betula pubescens. Flora 179: 55-83.

Keane, R. E., Hessburg, P. F., Landres, P. B. & Swanson, F. J. 2009. The use of historical range and variability (HRV) in landscape management. Forest Ecology and Management 258: 1025-1037.

Kern, C. C., Montgomery, R. A., Reich, P. B. & Strong, T. F. 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. Forest Science 60: 335-344.

Kimmins, J. P. (ed.) 1987. Forest Ecology. New York, NY: Macmillan Publishing Co. 531 p.

King, D. A. 2003. Allocation of above-ground growth is related to light in temperate deciduous saplings. Functional Ecology 17: 482-488.

Kinnaird, J. W. 1974. Effect of site conditions on the regeneration of birch (Betula pendula Roth and B. pubescens Ehrh.). Journal of Ecology 62: 467-472.

Kirchner, K., Kathke, S. & Bruelheide, H. 2011. The interaction of gap age and microsite for herb layer species in a near-natural spruce forest. Journal of Vegetation Science 22: 85-95.

Kneeshaw, D., Bergeron, Y. & Kuuluvainen, T. 2011. Forest Ecosystem Structure and Disturbance Dynamics across the Circumboreal Forest. (Chap. 14). In: Millington, A. & Blumler, M. A. (eds.). The SAGE Handbook of Biogeography. London: SAGE, pp. 261-278.

Koivula, M., Kuuluvainen, T., Hallman, E., Kouki, J., Siitonen, J. & Valkonen, S. 2014. Forest management inspired by natural disturbance dynamics (DISTDYN) – a long-term research and development project in Finland. Scandinavian Journal of Forest Research 29: 579-592.

Kooijman, A. M., Emmer, I. M., Fanta, J. & Sevink, J. 2000. Natural regeneration potential of the degraded Krkonose forests. Land Degradation and Development 11: 459-473.

Koski, V. & Tallqvist, R. 1978. Results of long-time measurements of the quantity of flowering and seed crop of forest trees. Folia Forestalia 364: 1-60.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research 16: 27-37.

Kozlowski, T. T. 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: Implications for forest management. Forest Ecology and Management 158: 195-221.

Kumela, H. & Hänninen, H. 2011. Metsänomistajien näkemykset metsänkäsittelymenetelmien monipuolistamisesta [Forest owners' views on the diversification of forest management approaches]. Metlan työraportteja / Working Papers of the Finnish Forest Research Institute 203: 76 p.

Kupferschmid, A. D. & Bugmann, H. 2005. Effect of microsites, logs and ungulate browsing on Picea abies regeneration in a mountain forest. Forest Ecology and Management 205: 251-265.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annales Zoologici Fennici 31: 35-51.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36: 97-125.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: The complexity challenge. Ambio 38: 309-315.

Kuuluvainen, T. & Aakala, T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fennica 45: 823–841.

Kuuluvainen, T. & Grenfell, R. 2012. Natural disturbance emulation in boreal forest ecosystem management - Theories, strategies, and a comparison with conventional even-aged management. Canadian Journal of Forest Research 42: 1185-1203.

Kuuluvainen, T., Hokkanen, T. J., Jarvinen, E. & Pukkala, T. 1993. Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation-soil system. Canadian Journal of Forest Research 23: 2101-2109.

Kuuluvainen, T., Järvinen, E., Hokkanen, T. J., Rouvinen, S. & Heikkinen, K. 1998a. Structural heterogeneity and spatial autocorrelation in a natural mature Pinus sylvestris dominated forest. Ecography 21: 159-174.

Kuuluvainen, T. & Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal Pinus sylvestris forest. Journal of Vegetation Science 9: 551-562.

Kuuluvainen, T. & Kalmari, R. 2003. Regeneration microsites of Picea abies seedlings in a windthrow area of a boreal old-growth forest in southern Finland. Annales Botanici Fennici 40: 401-413.

Kuuluvainen, T. & Pukkala, T. 1991. Interaction between canopy architecture and photosynthetically active direct radiation at different latitudes: simulation experiments and their ecological implications. In: Edelin, C. (ed.). L'arbre, biologie et développement: Proceedings of the 2nd international 'The tree' symposium held in Montpellier, 10-15 September. , pp. 277-291.

Kuuluvainen, T., Syrjänen, K. & Kalliola, R. 1998b. Structure of a pristine Picea abies forest in northeastern Europe. Journal of Vegetation Science 9: 563-574.

Lässig, R., Egli, S., Odermatt, O., Schönenberger, W., Stöckli, B. & Wohlgemuth, T. 1995. Beginn der Wiederbewaldung auf Windwurfflächen [The beginning of reforestation in windthrow areas]. Schweiz. Z. Forstwes. 146: 893-911.

Lawes, M. J. & Chapman, C. A. 2006. Does the herb Acanthus pubescens and/or elephants suppress tree regeneration in disturbed Afrotropical forest? Forest Ecology and Management 221: 278-284.

Leder, B. 1992. Weichlaubhölzer: Verjüngungsökologie, Jugendwachstum und Bedeutung in Jungbeständen der Hauptbaumarten Buche und Eiche. Landesanstalt für Forstwirtschaft Nordrhein-Westfalen-Sonderband. Balve: Zimmermann Druck und Verlag GmbH.

Leemans, R. 1990. Sapling establishment patterns in relation to light gaps in the canopy of two primeval pine-spruce forests in Sweden. In: Krahulec, F., Agnew, A. D. Q., Agnew, S. & Willems, H. J. (eds.). Spatial processes in plant communities. Proceedings of the workshop held in Liblice, September 1989. The Hague: SPB Academic Publishing, pp. 111-120.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (Picea abies L. Karst.) in two old-growth coniferous forests in central Sweden. Vegetatio 93: 157-165.

Lehto, J. 1956. Tutkimuksia mannyn luontaisesta uudistumisesta Etela-Suomen kangasmailla. [Studies on the natural reproduction of Scots pine on the upland soils of Southern Finland]. Acta Forestalia Fennica 66: 106.

Leikola, M., Raulo, J. & Pukkala, T. 1982. Männyn ja kuusen siemensadon vaihtelun ennustaminen [Predicting pine and spruce seed crop variability]. Folia Forestalia 537: 43.

Lindenmayer, D. & Franklin, J. F. 2002. Conserving forest biodiversity – A comprehensive multiscaled approach. Washington: Island Press.

Lindgren, K., Ekberg, I. & Eriksson, G. 1977. External factors influencing female flowering in Picea abies (L.) Karst. Studia Forestalia Suecica 142: 1-53.

Liu, Q. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval Picea abies forest. Journal of Vegetation Science 2: 391-402.

Lof, M. 2000. Establishment and growth in seedlings of Fagus sylvatica and Quercus robur: Influence of interference from herbaceous vegetation. Canadian Journal of Forest Research 30: 855-864.

Long, J. N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. Forest Ecology and Management 257: 1868-1873.

Lundmark, T., Bergh, J., Strand, M. & Koppel, A. 1998. Seasonal variation of maximum photochemical efficiency in boreal Norway spruce stands. Trees - Structure and Function 13: 63-67.

Malcolm, D. C., Mason, W. L. & Clarke, G. C. 2001. The transformation of conifer forests in Britain - Regeneration, gap size and silvicultural systems. Forest Ecology and Management 151: 7-23.

Mallik, A. U. 1994. Autecological response of Kalmia angustifolia to forest types and disturbance regimes. Forest Ecology and Management 65: 231-249.

Mallik, A. U., Kreutzweiser, D. P., Spalvieri, C. M. & Mackereth, R. W. 2013. Understory plant community resilience to partial harvesting in riparian buffers of central Canadian boreal forests. Forest Ecology and Management 289: 209-218.

Mallik, A. U. & Pellissier, F. 2000. Effects of Vaccinium myrtillus on spruce regeneration: Testing the notion of coevolutionary significance of allelopathy. Journal of Chemical Ecology 26: 2197-2209.

Mallik, A. U., Wang, J. W., Seigwart-Collier, L. & Roberts, B. R. 2012. Morphological and ecophysiological responses of sheep laurel (Kalmia angustifolia L.) to shade. Forestry 85: 513-522.

Man, R., Kayahara, G. J., Rice, J. A. & MacDonald, G. B. 2008. Eleven-year responses of a boreal mixedwood stand to partial harvesting: Light, vegetation, and regeneration dynamics. Forest Ecology and Management 255: 697-706.

Man, R., Rice, J. A. & MacDonald, G. B. 2009. Long-term response of planted conifers, natural regeneration, and vegetation to harvesting, scalping, and weeding on a boreal mixedwood site. Forest Ecology and Management 258: 1225-1234.

Marrs, R. H. & Watt, A. S. 2006. Biological flora of the British Isles: Pteridium aquilinum (L.) Kuhn. Journal of Ecology 94: 1272-1321.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66: 185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - Trends in space and successional time. Journal of Ecology 82: 113-123.

Matlack, G. R. & Litvaitis, J. A. 1999. Forest edges. In: Hunter, J., M.L. (ed.). Maintaining Biodiversity in Forest Ecosystems. Cambridge: Cambridge University Press, pp. 210-233.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environmental Reviews 9: 1-59.

Messier, C., Puettmann, K. J. & Coates, K. D. (eds.) 2013. Managing forests as complex adaptive systems: Building resilience to the challenge of global change. New York, NY: Routledge. 1-354 p.

Miina, J., Pukkala, T., Hotanen, J. P. & Salo, K. 2010. Optimizing the joint production of timber and bilberries. Forest Ecology and Management 259: 2065-2071.

Milborrow, S. 2015. plotmo: Plot a Model's Response and Residuals. R package version 3.1.3. .

Moffatt, S. F. & McLachlan, S. M. 2004. Understorey indicators of disturbance for riparian forests along an urban-rural gradient in Manitoba. Ecological Indicators 4: 1-16.

Moser, O. 1965. Untersuchungen über die Abhängigkeit der natürlichen Verjüngung der Fichte vom Standort. Cbl. Ges. Forstwesen 82: 18-55.

Motta, R., Berretti, R., Lingua, E. & Piussi, P. 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. Forest Ecology and Management 235: 155-163.

Nakamura, T. 1992. Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan. Ecological Research 7: 155-162.

Nakashizuka, T. 1985. Diffused light conditions in canopy gaps in a beech (Fagus crenata Blume) forest. Oecologia 66: 472-474.

Narukawa, Y. & Yamamoto, S. I. 2001. Gap formation, microsite variation and the conifer seedling occurrence in a subalpine old-growth forest, central Japan. Ecological Research 16: 617-625.

Nikkanen, T. & Ruotsalainen, S. 2000. Variation in flowering abundance and its impact on the genetic diversity of the seed crop in a Norway spruce seed orchard. Silva Fennica 34: 205-222.

Nilsson, M. C., Hogberg, P., Zackrisson, O. & Wang Fengyou 1993. Allelopathic effects by Empetrum hermaphroditum on development and nitrogen uptake by roots and mycorrhizae of Pinus silvestris. Canadian Journal of Botany 71: 620-628.

Nilsson, M. C., Steijlen, I. & Zackrisson, O. 1996. Time-restricted seed regeneration of Scots pine in sites dominated by feather moss after clear-cutting. Canadian Journal of Forest Research 26: 945-953.

Nilsson, M. C. & Wardle, D. A. 2005. Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment 3: 421-428.

Nilsson, M. C., Wardle, D. A. & Dahlberg, A. 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. Oikos 86: 16-26.

Nilsson, M. C. & Zackrisson, O. 1992. Inhibition of Scots pine seedling establishment by Empetrum hermaphroditum. Journal of Chemical Ecology 18: 1857-1870.

Nilsson, U., Gemmel, P., Johansson, U., Karlsson, M. & Welander, T. 2002. Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. Forest Ecology and Management 161: 133-145.

Oechel, W. C. & Van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the taiga. In: Van Cleve, K., Chapin III, F. S., Flanagan, P. W., Viereck, L. A. & Dyrness, C. T. (eds.). Forest Ecosystems in the Alaskan Taiga. New York, NY: Springer Verlag, pp. 121-137.

Ohlson, M. 1995. Growth and nutrient characteristics in bog and fen populations of Scots pine (Pinus sylvestris). Plant and Soil 172: 235-245.

Ohlson, M. & Zackrisson, O. 1992. Tree establishment and microhabitat relationships in north Swedish peatlands. Canadian Journal of Forest Research 22: 1869-1877.

Oliver, C. D. 1980. Forest development in North America following major disturbances. Forest Ecology and Management 3: 153-168.

Olsson, B. A. & Staaf, H. 1995. Influence of harvesting intensity of logging residues on ground vegetation in coniferous forests. Journal of Applied Ecology 32: 640-654.

Örlander, G. & Karlsson, K. 2000. Influence of shelterwood density on survival and height increment of Picea abies advance growth. Scandinavian Journal of Forest Research 15: 20-29.

Örlander, G., Nilsson, U. & Hällgren, J. E. 1996. Competition for water and nutrients between ground vegetation and planted Picea abies. New Zealand Journal of Forestry Science 26: 99-117.

Pages, J. P. & Michalet, R. 2003. A test of the indirect facilitation model in a temperate hardwood forest of the northern French Alps. Journal of Ecology 91: 932-940.

Pakarinen, P. & Rinne, R. J. K. 1979. Growth rates and heavy metal concentrations of five moss species in paludified spruce forests. Lindbergia 5: 77-83.

Palik, B. J., Mitchell, R. J., Houseal, G. & Pederson, N. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Canadian Journal of Forest Research 27: 1458-1464.

Palmer, M. W. & Dixon, P. M. 1990. Small-Scale Environmental Heterogeneity and the Analysis of Species Distributions along Gradients. Journal of Vegetation Science 1: 57-65.

Pellissier, F. 1993. Allelopathic inhibition of spruce germination. Acta Oecologica 14: 211-218.

Perala, D. A. & Alm, A. A. 1990a. Regeneration silviculture of birch: A review. Forest Ecology and Management 32: 39-77.

Perala, D. A. & Alm, A. A. 1990b. Reproductive ecology of birch: A review. Forest Ecology and Management 32: 1-38.

Perera, A. H., Buse, L. J. & Weber, M. G. 2004. Emulating natural forest landscape disturbances – Concepts and applications. New York: Columbia University Press.

Picon-Cochard, C., Coll, L. & Balandier, P. 2006. The role of below-ground competition during early stages of secondary succession: The case of 3-year-old Scots pine (Pinus sylvestris L.) seedlings in an abandoned grassland. Oecologia 148: 373-383.

Poulson, T. L. & Platt, W. J. 1989. Gap light regimes influence canopy tree diversity. Ecology 70: 553-555.

Prévost, M., Raymond, P. & Lussier, J. M. 2010. Regeneration dynamics after patch cutting and scarification in yellow birch-conifer stands. Canadian Journal of Forest Research 40: 357-369.

Pröll, G., Darabant, A., Gratzer, G. & Katzensteiner, K. 2015. Unfavourable microsites, competing vegetation and browsing restrict post-disturbance tree regeneration on extreme sites in the Northern Calcareous Alps. European Journal of Forest Research 134: 293-308.

Puettmann, K. J., Coates, K. D. & Messier, C. 2009. A critique of silviculture: managing for complexity. Ecological Restoration 28: 99-101.

Pukkala, T. 1987. A model for predicting the seed crop of Picea abies and Pinus sylvestris. Silva Fennica 21: 135-144.

Pukkala, T., Hokkanen, T. & Nikkanen, T. 2010. Prediction models for the annual seed crop of Norway spruce and Scots pine in Finland. Silva Fennica 44: 629-642.

Pukkala, T. & Kolström, T. 1992. A stochastic spatial regeneration model for Pinus sylvestris. Scandinavian Journal of Forest Research 7: 377-385.

Pukkala, T., Lähde, E. & Laiho, O. 2011. Metsän jatkuva kasvatus [Uneven-aged forest management]. Joensuu: Joen Forest Program Consulting.

R Core Team 2014. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Raich, J. W. & Gong, W. K. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. Journal of Tropical Ecology 6: 203-217.

Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. 2010. The 2010 Red List of Finnish Species. Helsinki: Ympäristöministeriö & Suomen ympäristökeskus. 685 p.

Raunio, A., Schulman, A. & Kontula, T. (eds.) 2008. Suomen luontotyyppien uhanalaisuus - Osa 1: Tulokset ja arvioinnin perusteet. 8 edition. Suomen ympäristö. 75-109 p.

Ren, J. Y., Kadir, A. & Yue, M. 2015. The role of tree-fall gaps in the natural regeneration of birch forests in the Taibai Mountains. Applied Vegetation Science 18: 64-74.

Repo, T. 1992. Seasonal changes of frost hardiness in Picea abies and Pinus sylvestris in Finland. Canadian Journal of Forest Research 22: 1949-1957.

Revelle, W. 2015. psych: Procedures for Personality and Psychological Research. Evanston, Illinois, USA: Northwestern University.

Robert, E., Brais, S., Harvey, B. D. & Greene, D. 2012. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. Canadian Journal of Forest Research 42: 1446-1455.

Robic, D. 1985. Some problems of natural regeneration in man-made spruce forest of upper mountain belt in Pohorje. Zb. Gozd. Lesar. 26: 149-159.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62: 1041-1051.

Runkle, J. R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. Ecology 79: 1768-1780.

Runkle, J. R. & Yetter, T. C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. Ecology 68: 417-424.

Russell, A. E., Raich, J. W. & Vitousek, P. M. 1998. The ecology of the climbing fern Dicranopteris linearis on windward Mauna Loa, Hawaii. Journal of Ecology 86: 765-779.

Sarkar, D. 2008. Lattice: Multivariate Data Visualization with R. New York, NY: Springer.

Sarvas, R. 1948. A research on the regeneration of birch in south Finland. Commun. Inst. For. Fenn. 35: 1-91.

Schrötter, H. 1998. Waldbau mit Birke: Gegebenheiten und Erfordernisse in Mecklenburg-Vorpommern. Forst und Holz 4: 105-111.

Schumann, M. E., White, A. S. & Witham, J. W. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. Forest Ecology and Management 176: 543-561.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399-409.

Selås, V., Piovesan, G., Adams, J. M. & Bernabei, M. 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. Canadian Journal of Forest Research 32: 217-225.

Sernander, R. 1936. The primitive forests of Granskär och Fiby: a study of the part played by storm gaps and dwarf trees in the regeneration of the Swedish spruce forest. Acta Phytogeographica Suecica 8: 1-232.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: A review with special reference to Russian studies. Annals of Forest Science 66: 201p1-201p10.

Sipe, T. W. & Bazzaz, F. A. 1995. Gap partitioning among maples (Acer) in central New England: Survival and growth. Ecology 76: 1587-1602.

Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta For.Fenn. 62: 1-363.

Skoklefald, S. 1992a. Engangsundersøkelser i frøtrestillinger av furu. Rapport fra Skogforsk 14: 5-14.

Skoklefald, S. 1992b, Naturlig Foryngelse av Gran og Furu [Natural Regeneration of Pine]. Norwegian Forest Research Institute.

Skvortsova, E. B., Ulanova, N. G. & Basevich, V. F. 1983. Ecological role of windfalls. Moscow: Lesnaya promyshlennost'.

Sollins, P., Cline, S. P., Verhoeven, T., Sachs, D. & Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 1585-1595.

Spence, J. R. 2001. The new boreal forestry: Adjusting timber management to accommodate biodiversity. Trends in Ecology and Evolution 16: 591-593.

Steijlen, I., Nilsson, M. C. & Zackrisson, O. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. Canadian Journal of Forest Research 25: 713-723.

Stewart, K. J. & Mallik, A. U. 2006. Bryophyte responses to microclimatic edge effects across riparian buffers. Ecological Applications 16: 1474-1486.

Szewczyk, J. & Szwagrzyk, J. 1996. Tree regeneration on rotten wood and on soil in old-growth stand. Vegetatio 122: 37-46.

Takahashi, K. 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understorey. Journal of Vegetation Science 8: 529-536.

Taskinen, O., Ilvesniemi, H., Kuuluvainen, T. & Leinonen, K. 2003. Response of fine roots to an experimental gap in a boreal Picea abies forest. Plant and Soil 255: 503-512.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J. S., Stokland, J. N., Sverdrup-Thygeson, A. & Mönkkönen, M. 2010. Woodland key habitats in northern Europe: Concepts, inventory and protection. Scandinavian Journal of Forest Research 25: 309-324.

Tømmervik, H., Johansen, B., Tombre, I., Thannheiser, D., Høgda, K. A., Gaare, E. & Wielgolaski, F. E. 2004. Vegetation changes in the Nordic mountain birch forest: The influence of grazing and climate change. Arctic, Antarctic, and Alpine Research 36: 323-332.

Tømmervik, H., Wielgolaski, F. E., Neuvonen, S., Solberg, B. & Høgda S, K. A. 2005. Biomass and production on a landscape level in the northern mountain birch forests. In: Wielgolaski, F. E. (ed.). Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests. Heidelberg, Germany: Springer, pp. 53-70.

Tonteri, T. 1994. Species richness of boreal understorey forest vegetation in relation to site type and successional factors. Annales Zoologici Fennici 31: 53-60.

Tremblay, G. D. & Boudreau, S. 2011. Black spruce regeneration at the treeline ecotone: Synergistic impacts of climate change and caribou activity. Canadian Journal of Forest Research 41: 460-468.

Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: A review. Forest Ecology and Management 135: 155-167.

Vaartaja, O. 1952. Forest humus quality and light conditions as factors influencing damping-off. Phytopathology 42: 501-506.

Valkeapää, A., Paloniemi, R., Vainio, A., Vehkalahti, K., Helkama, K., Karppinen, H., Kuuluvainen, J., Ojala, A., Rantala, T. & Rekola, M. 2009, Suomen metsät ja metsäpolitiikka – kansalaisten näkemyksiä [Finnish forests and forest policy - people's views.]. Reports 2009 55. University of Helsinki, Department of Forest Economics.

Valkonen, S. & Maguire, D. 2005. Relationship between seedbed properties and the emergence of spruce germinants in recently cut Norway spruce selection stands in Southern Finland. For Ecol Manag 210: 255-266.

Valkonen, S., Sirén, M. & Piri, T. (eds.) 2010. Poiminta- ja pienaukkohakkuut – vaihtoehtoja avohakkuulle [Selection and gap felling – alternatives for clear felling]. Metsäkustannus.

Valkonen, S., Koskinen, K., Mäkinen, J. & Vanha-Majamaa, I. 2011. Natural regeneration in patch clear-cutting in Picea abies stands in Southern Finland. Scandinavian Journal of Forest Research 26: 530-542.

Vanhatalo, V., Leinonen, K., Rita, H. & Nygren, M. 1996. Effect of prechilling on the dormancy of Betula pendula seeds. Canadian Journal of Forest Research 26: 1203-1208.

Veer, M. A. C. & Kooijman, A. M. 1997. Effects of grass-encroachment on vegetation and soil in Dutch dry dune grassland. Plant and Soil 192: 119-128.

Vodde, F., Jõgiste, K., Gruson, L., Ilisson, T., Köster, K. & Stanturf, J. A. 2010. Regeneration in windthrow areas in hemiboreal forests: The influence of microsite on the height growths of different tree species. Journal of Forest Research 15: 55-64.

Vodde, F., Jõgiste, K., Kubota, Y., Kuuluvainen, T., Köster, K., Lukjanova, A., Metslaid, M. & Yoshida, T. 2011. The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest. Journal of Forest Research 16: 155-167.

Vodde, F., Jõgiste, K., Engelhart, J., Frelich, L. E., Moser, W. K., Sims, A. & Metslaid, M. 2015. Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: Results from the first post-storm decade. Forest Ecology and Management 348: 174-185.

Wagner, S., Wälder, K., Ribbens, E. & Zeibig, A. 2004. Directionality in fruit dispersal models for anemochorous forest trees. Ecological Modelling 179: 487-498.

Wardle, D. A., Nilsson, M. C., Zackrisson, O. & Gallet, C. 2003. Determinants of litter mixing effects in a Swedish boreal forest. Soil Biology and Biochemistry 35: 827-835.

Wayne, P. M. & Bazzaz, F. A. 1993a. Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology 74: 1500-1515.

Wayne, P. M. & Bazzaz, F. A. 1993b. Morning vs afternoon sun patches in experimental forest gaps: consequences of temporal incongruency of resources to birch regeneration. Oecologia 94: 235-243.

Whitmore, T. C. 1978. Canopy gaps and the two major groups of forest trees. Ecology 70 (3): 536–538.

Wickham, H. 2011. The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software 40 (1): 1-29.

Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73 (1): 3-36.

Yamamoto, S. I. 2000. Forest gap dynamics and tree regeneration. Canadian Journal of Forest Research 5 (4): 223–229.

Yli-Vakkuri, P. 1963. Experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands. Acta For.Fenn. 75: 1-122.

York, R. A., Battles, J. J. & Heald, R. C. 2003. Edge effects in mixed conifer group selection openings: Tree height response to resource gradients. Forest Ecology and Management 179: 107-121.

Zackrisson, O. & Nilsson, M. C. 1992. Allelopathic effects by Empetrum hermaphroditum on seed germination of two boreal tree species. Canadian Journal of Forest Research 22: 1310-1319.

Zackrisson, O., Nilsson, M. C., Dahlberg, A. & Jäderlund, A. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos 78: 209-220.

Zackrisson, O., Nilsson, M. C., Jäderlund, A. & Wardle, D. A. 1999. Nutritional effects of seed fall during mast years in boreal forest. Oikos 84: 17-26.

Zackrisson, O., Nilsson, M. C., Steijlen, I. & Hornberg, G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. Journal of Ecology 83: 469-483.

Zasada, J. C., Sharik, T. L. & Nygren, M. 1992. The reproductive process in boreal forest trees. In: Bonan, G. B. (ed.). A Systems Analysis of the Global Boreal Forest. Cambridge: Cambridge University Press, pp. 85-125.

Zielonka, T. 2006. When does dead wood turn into a substrate for spruce replacement? Journal of Vegetation Science 17: 739-746.

Zielonka, T. & Niklasson, M. 2001. Dynamics of dead wood and regeneration pattern in natural spruce forest in the Tatra Mountains, Poland. Ecol. Bull. 49: 159-163.

Zielonka, T. & Piątek, G. 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. Plant Ecology 172: 63-72.

Zimmerman, J. K., Pulliam, W. M., Lodge, D. J., Quinones-Orfila, V., Fetcher, N., Guzman-Grajales, S., Parrotta, J. A., Asbury, C. E., Walker, L. R. & Waide, R. B. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos 72: 314-322.

APPENDICES

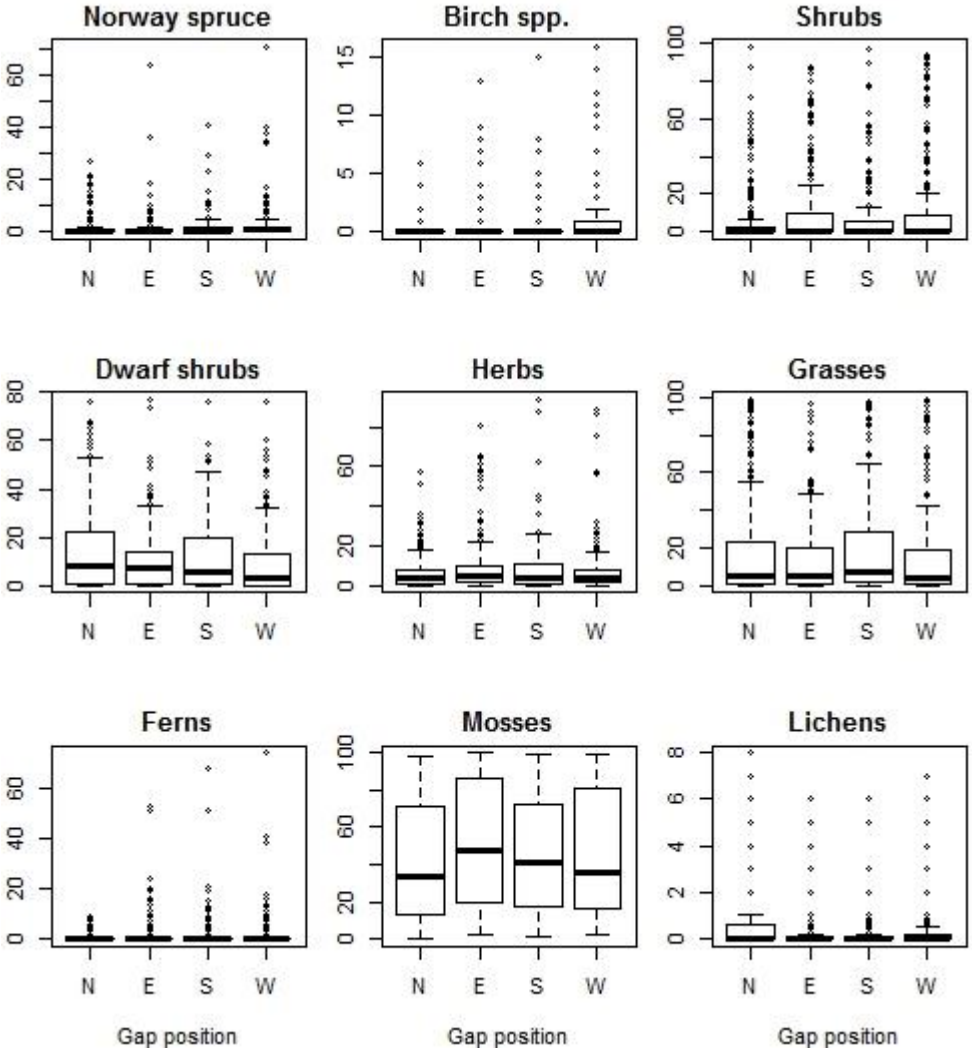
Appendix 1. Pearson's coefficients of correlation between seedlings, vegetation and all possible response variables

	Spruce	Birch	Distance	Shrubs	Dwarf shrubs	Herbs	Grasses	Ferns	Mosses	Lichens
Spruce	1	0.30	-0.05	-0.07	-0.07	-0.01	-0.10	0.01	0.09	0.00
Birch	0.30	1	0.04	0.05	-0.04	0.02	-0.05	-0.01	-0.03	0.00
Distance	-0.05	0.04	1	0.36	-0.24	0.29	0.41	0.10	-0.54	-0.03
Shrubs	-0.07	0.05	0.36	1	-0.29	0.16	0.02	0.09	-0.35	-0.03
Dwarf shrubs	-0.07	-0.04	-0.24	-0.29	1	-0.25	-0.35	-0.12	0.35	-0.05
Herbs	-0.01	0.02	0.29	0.16	-0.25	1	0.01	0.05	-0.25	-0.05
Grasses	-0.10	-0.05	0.41	0.02	-0.35	0.01	1	0.00	-0.47	-0.09
Ferns	0.01	-0.01	0.10	0.09	-0.12	0.05	0.00	1	-0.11	-0.05
Mosses	0.09	-0.03	-0.54	-0.35	0.35	-0.25	-0.47	-0.11	1	-0.02
Lichens	0.00	0.00	-0.03	-0.03	-0.05	-0.05	-0.09	-0.05	-0.02	1
Tree base	0.01	-0.03	-0.18	-0.09	-0.06	-0.03	-0.11	0.00	-0.05	0.29
Stumps (young)	0.03	0.16	0.16	0.18	-0.06	0.02	-0.04	0.01	-0.10	0.18
Stumps (decayed)	0.04	0.07	-0.07	0.03	0.02	-0.04	-0.07	-0.02	0.01	0.04
Logs	0.02	0.02	0.14	0.22	-0.19	0.11	-0.01	0.07	-0.22	0.17
Stone (covered)	-0.08	0.00	-0.03	-0.07	0.20	0.03	-0.27	0.00	0.27	0.01
Stone (bare)	-0.02	-0.01	0.07	-0.03	-0.08	0.03	-0.05	0.02	-0.05	0.18
Duff	-0.03	0.02	0.15	0.36	-0.24	0.14	0.25	0.09	-0.50	-0.01
Slash	0.08	0.01	0.19	0.29	-0.21	0.19	0.05	0.09	-0.32	-0.02
Mineral soil	-0.02	-0.01	0.05	-0.02	-0.03	-0.02	-0.02	-0.01	-0.05	-0.02
Humus	-0.03	-0.02	0.02	0.09	-0.07	0.03	-0.05	-0.02	-0.09	0.02

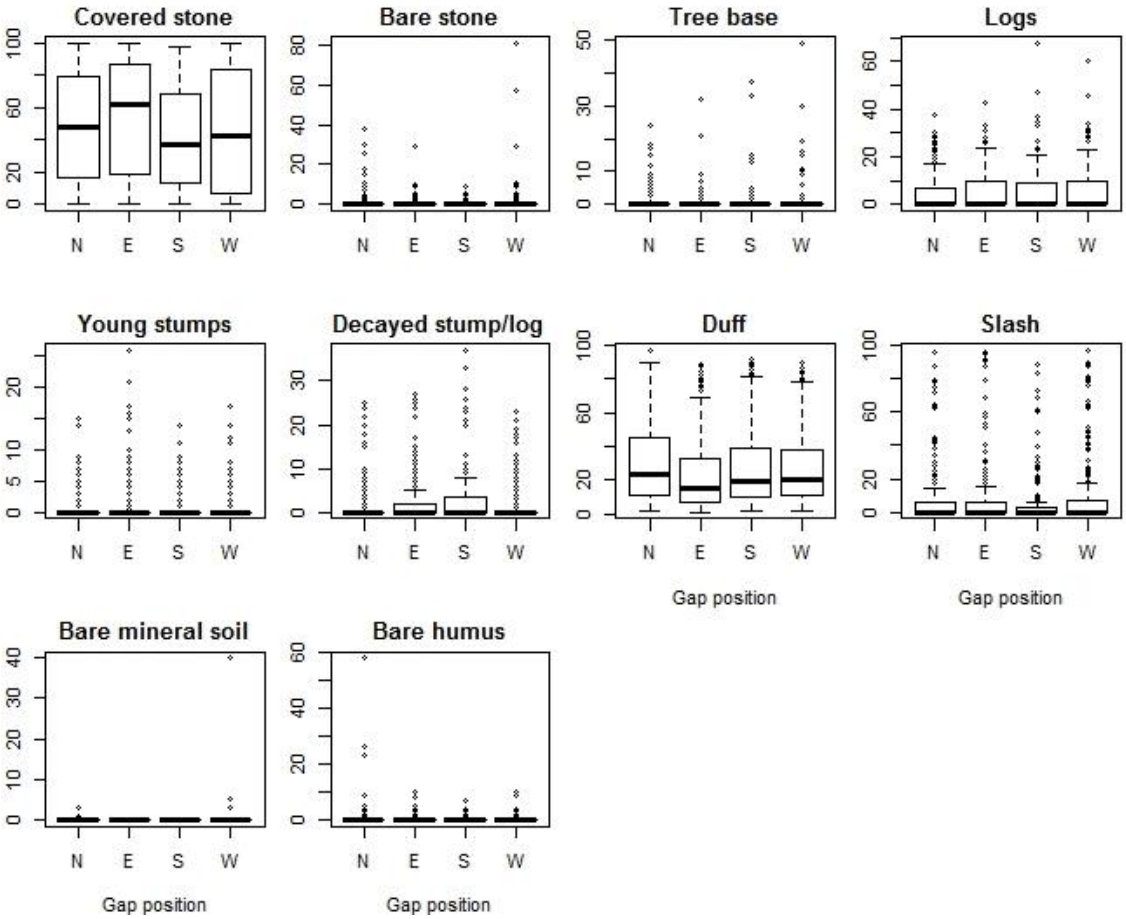
Appendix 2. Pearson's coefficients of correlation between microsite types and all possible response variables

	Tree base	Stumps (young)	Stumps (decayed)	Logs	Stone (covered)	Stone (bare)	Duff	Slash	Mineral soil	Humus
Spruce	0.01	0.03	0.04	0.02	-0.08	-0.02	-0.03	0.08	-0.02	-0.03
Birch	-0.03	0.16	0.07	0.02	0.00	-0.01	0.02	0.01	-0.01	-0.02
Distance	-0.18	0.16	-0.07	0.14	-0.03	0.07	0.15	0.19	0.05	0.02
Shrubs	-0.09	0.18	0.03	0.22	-0.07	-0.03	0.36	0.29	-0.02	0.09
Dwarf shrubs	-0.06	-0.06	0.02	-0.19	0.20	-0.08	-0.24	-0.21	-0.03	-0.07
Herbs	-0.03	0.02	-0.04	0.11	0.03	0.03	0.14	0.19	-0.02	0.03
Grasses	-0.11	-0.04	-0.07	-0.01	-0.27	-0.05	0.25	0.05	-0.02	-0.05
Ferns	0.00	0.01	-0.02	0.07	0.00	0.02	0.09	0.09	-0.01	-0.02
Mosses	-0.05	-0.10	0.01	-0.22	0.27	-0.05	-0.50	-0.32	-0.05	-0.09
Lichens	0.29	0.18	0.04	0.17	0.01	0.18	-0.01	-0.02	-0.02	0.02
Tree base	1	-0.06	0.01	0.14	-0.15	-0.01	0.08	-0.04	-0.01	-0.01
Stumps (young)	-0.06	1	-0.06	0.19	-0.08	-0.03	0.02	0.06	-0.01	-0.02
Stumps (decayed)	0.01	-0.06	1	-0.04	-0.14	-0.05	-0.02	-0.10	-0.01	0.01
Logs	0.14	0.19	-0.04	1	-0.14	-0.04	0.12	0.16	-0.02	-0.02
Stone (covered)	-0.15	-0.08	-0.14	-0.14	1	0.05	-0.25	-0.19	-0.02	-0.06
Stone (bare)	-0.01	-0.03	-0.05	-0.04	0.05	1	-0.06	-0.04	0.48	0.17
Duff	0.08	0.02	-0.02	0.12	-0.25	-0.06	1	0.25	-0.03	0.01
Slash	-0.04	0.06	-0.10	0.16	-0.19	-0.04	0.25	1	-0.02	0.08
Mineral soil	-0.01	-0.01	-0.01	-0.02	-0.02	0.48	-0.03	-0.02	1	0.06
Humus	-0.01	-0.02	0.01	-0.02	-0.06	0.17	0.01	0.08	0.06	1

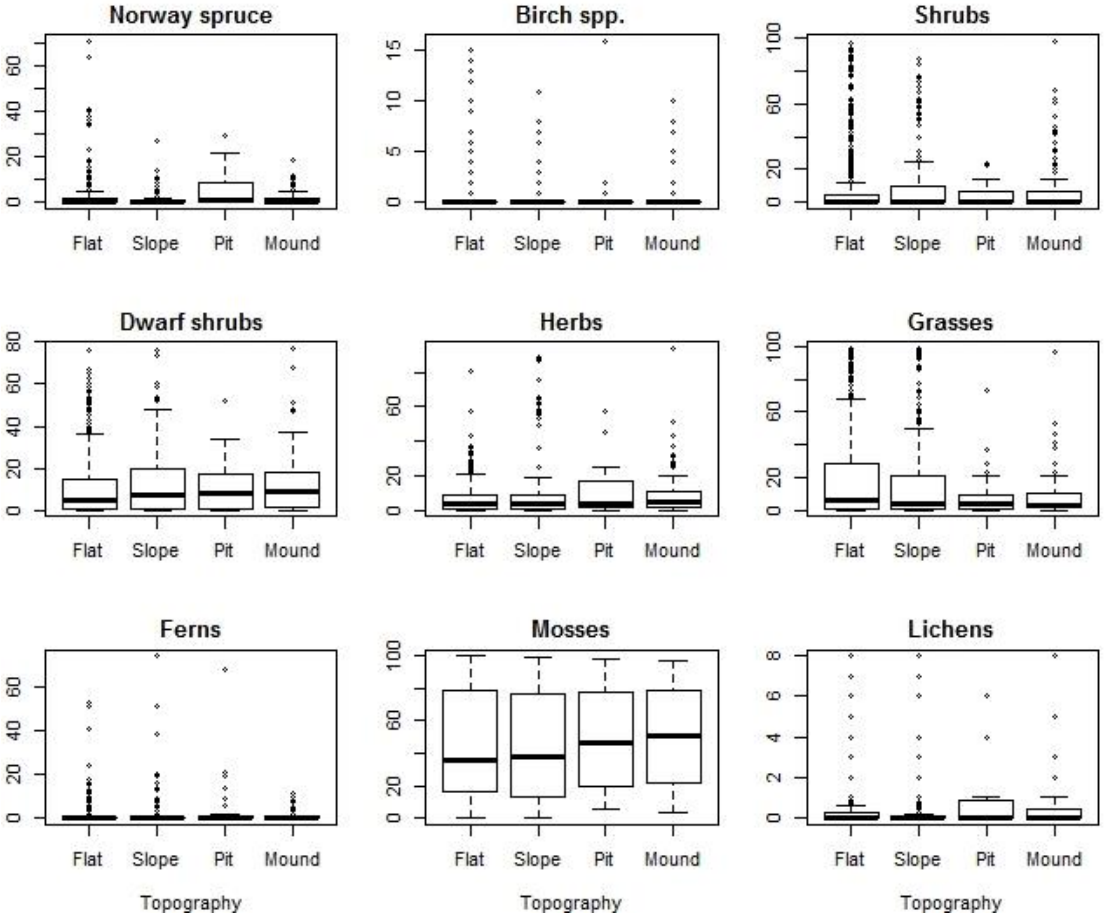
Appendix 3. Boxplots of seedling densities and vegetation covers at each gap position



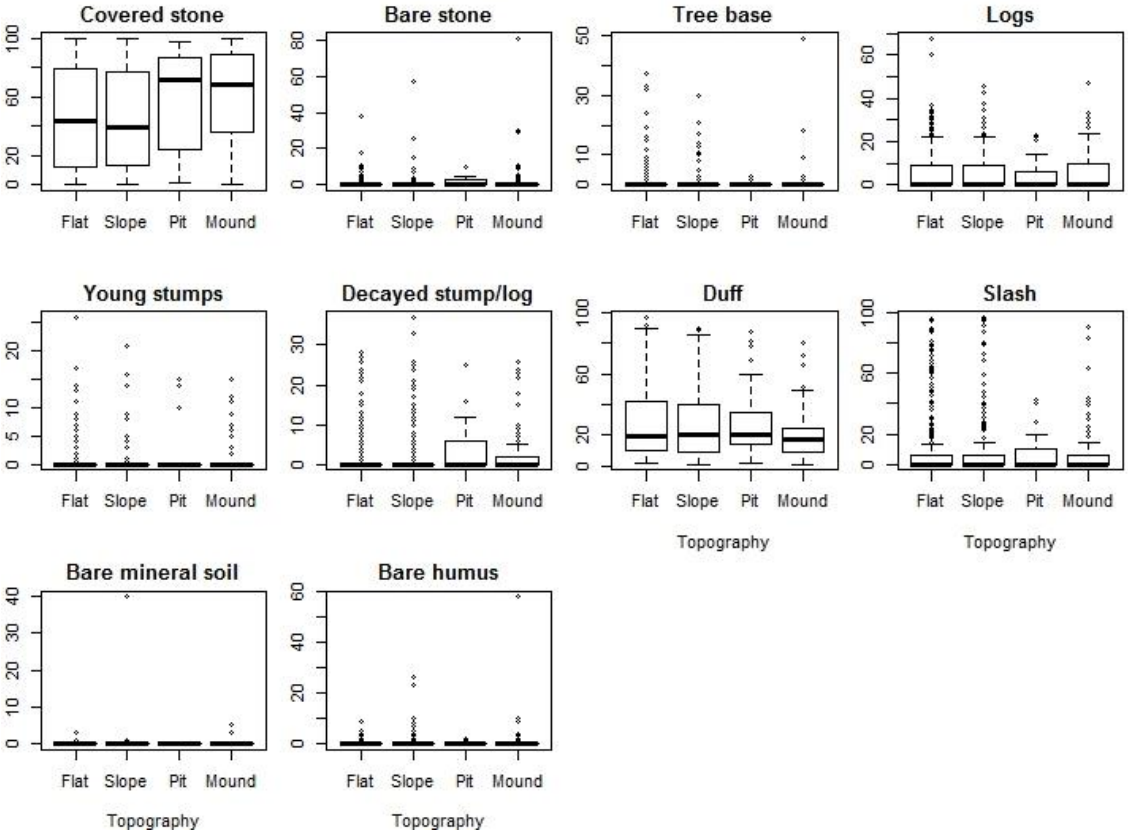
Appendix 4. Boxplots of microsite covers at each gap position



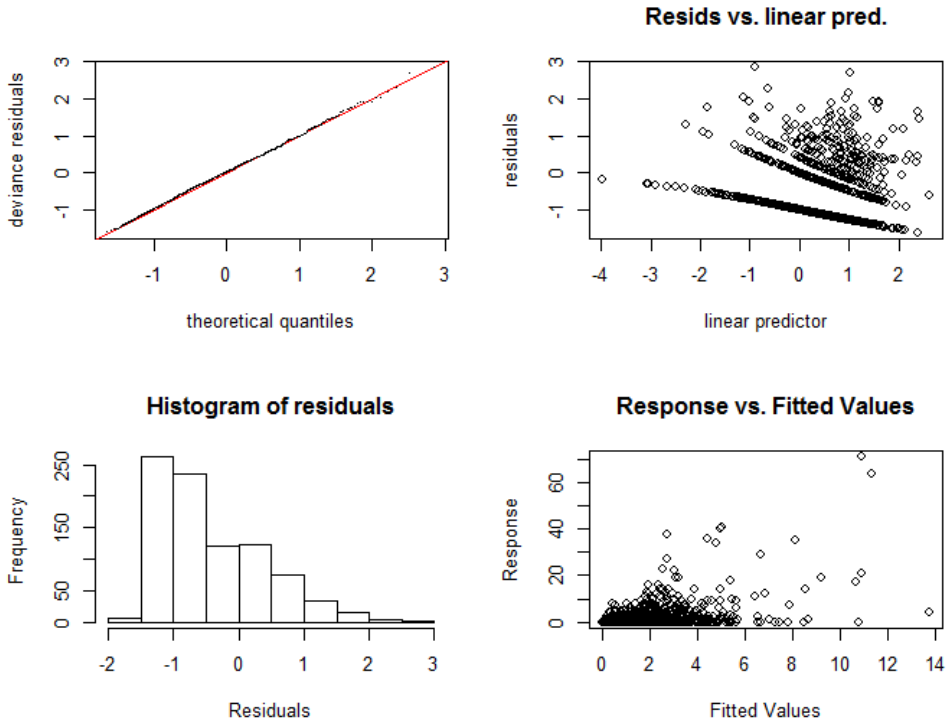
Appendix 5. Boxplots of seedling densities and vegetation covers across each topography type



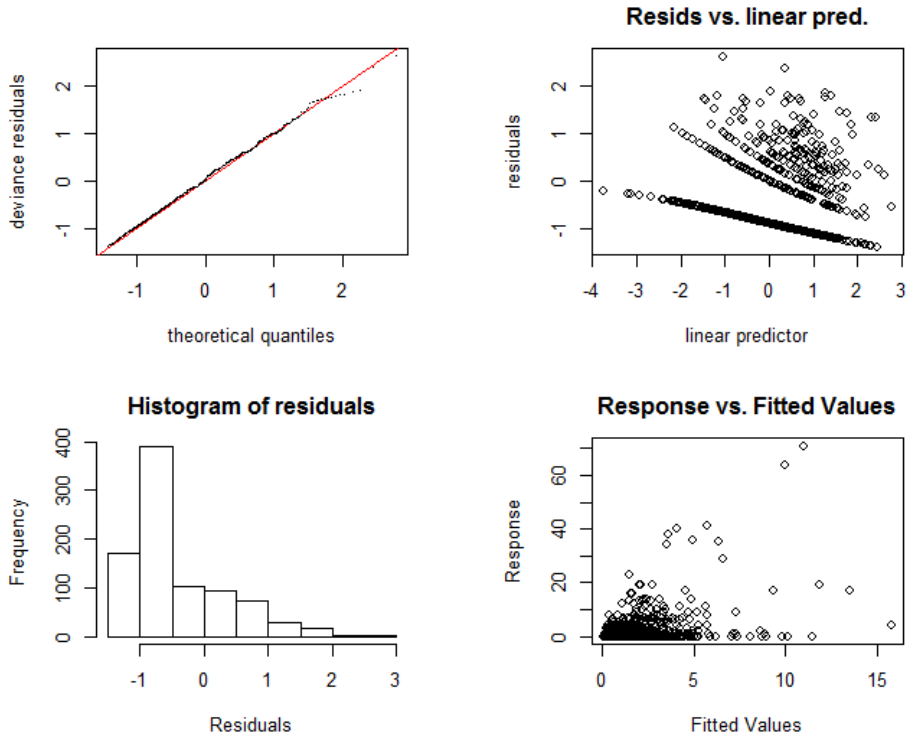
Appendix 6. Boxplots of microsite covers across each topography type



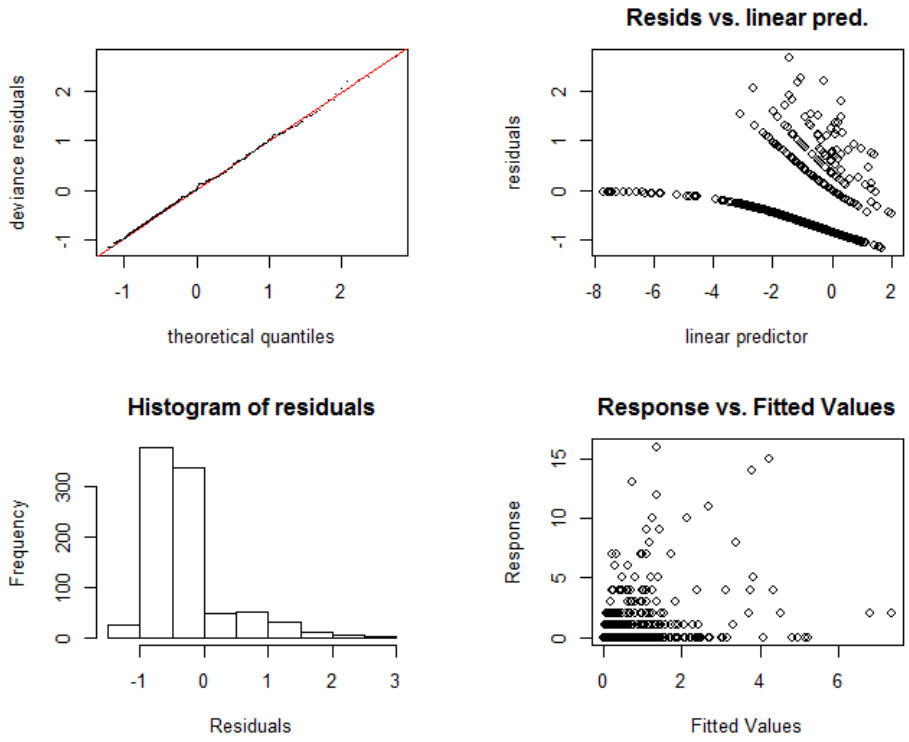
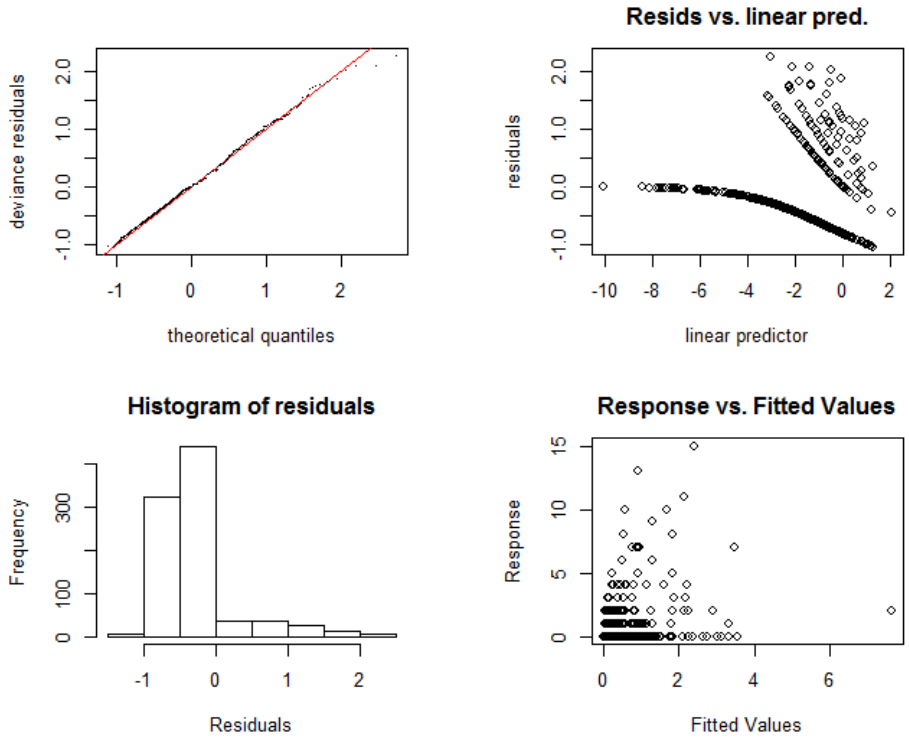
Appendix 7. Diagnostic plots of the GAM for the number of Norway spruce seedlings per m^2



Appendix 8. Diagnostic plots of the GAM for the number of Norway spruce seedlings per m^2 which emerged after harvest



Appendix 9. Diagnostic plots of the GAM for the number of birch seedlings per m^2



Appendix 10. Diagnostic plots of the GAM for the number of birch seedlings per m^2 which emerged after harvest