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**Natural tree regeneration and vegetation dynamics across harvest gaps in Norway spruce –
dominated forests in Southern Finland**

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Abstract

We analysed the impact of forest gap characteristics and understory vegetation on the natural regeneration patterns of Norway spruce and birch. The gaps were located in spruce-dominated forests in Southern Finland, and had been established by harvesting 4–5 growing seasons earlier. Their diameters ranged from 30–60m. In order to analyze the complex patterns of multiple factors simultaneously, we analysed the data using generalized additive models. The models included gradients related to distance from gap (forest) edge, cardinal position in the gap, understory vegetation, microsite types and microtopography. The high number of seedlings inside the gaps suggests promising regeneration potential—some 20.3 spruce and 6.8 birch seedlings per m². The 0–15m zone into the gap supported the greatest seedling abundance. Gap centers (15m+) fostered a highly competitive environment, and hosted much lower seedling densities. Northern gap positions varied most significantly, supporting fewer birch seedlings, and greater covers of grasses and dwarf shrubs. The results indicate that harvested forest gaps should have diameters less than 40m (at least initially) in order to prevent excessive proliferation of understory vegetation and to facilitate seedling emergence across the gaps under similar conditions.

Key words: Natural regeneration, boreal forest, understory vegetation, gap, microsite

41 **Introduction**

42 Gap harvesting is among the main harvesting methods employed in uneven-aged forest
43 management of Norway spruce (*Picea abies* (L.) Karst.)–dominated stands in the Nordic region.
44 This method, and uneven-aged forest management as a whole, is quite novel in the region, and as
45 such very little experience and research-based knowledge is available for practitioners and
46 scientists. Forest gaps tend to promote natural tree regeneration by establishing environmental
47 conditions suitable for the recruitment, survival and growth of tree seedlings (Liu and Hytteborn
48 1991, Kuuluvainen 1994). The factors influencing tree regeneration are related to the newly
49 established gradients across the gap in terms of light, temperature, moisture, competition from
50 trees in the gap edge zone, and seed crops. Variations in light, moisture and temperature across
51 the gap are largely controlled by variations in incoming solar radiation. The patterns of solar
52 radiation vary according to the cardinal position in the gap (N, S, E, or W), with the greatest
53 levels of radiation occurring at the northern-central gap positions (Canham et al. 1990, Raymond
54 et al. 2006). Within northern latitudes, this effect also extends into the residual stand, where
55 radiation levels can be as high as 50% of the incoming radiation in the northern gap edge
56 positions (De Chantal et al. 2003). Forest gaps also include a large range of microsite types (e.g.
57 bare mineral soil, stumps), all of which play a central role in the success of tree seedling
58 establishment and growth (Zasada et al. 1992, Kuuluvainen 1994, Hanssen 2002, 2003). These
59 microsite conditions affect regeneration in variable ways, and the effects often vary among tree
60 species (Grenfell et al. 2011).

61 These environmental gradients also greatly influence the patterns of understory vegetation
62 composition across the gap. Understory vegetation can play a critical role especially in early
63 post-harvest tree regeneration dynamics, since as a whole understory vegetation is able to

respond quite rapidly (3–5 years) to the new post-harvest conditions (Hill et al. 2005, Stewart and Mallik 2006, Vanha-Majamaa et al. 2017). Species groups that increase in cover after harvesting include shrubs, grasses and sedges, and early successional light-demanding herb species (Grushecky and Fajvan 1999, Domke et al. 2007). Understory vegetation is also very sensitive to variations in microsite conditions, topography and resource availability, and the patterns of plant species regeneration reflect this (Palmer and Dixon 1990, Tonteri 1994, Halpern et al. 2005). As a result, vegetation species composition usually displays quite variable spatio-temporal dynamics and compositional patterns. As natural regeneration progresses, the intensifying competition from understory vegetation and other seedlings also greatly affect the patterns of tree regeneration (e.g., Kuuluvainen 1994, Huggard and Vyse 2002, Hanssen 2003, Valkonen et al. 2011). Consequently, understory vegetation can be an important tool for revealing the finer-scale nuances of gap-level heterogeneity, and can help to better understand the processes affecting seedling regeneration across gaps.

Previous studies have often focused only on the most obvious factors affecting tree regeneration in gaps (Valkonen et al. 2011, Valkonen and Siitonen 2016). When specifically targeted, the effects of the factors controlling regeneration have been researched either individually, or in conjunction with only a small number of factors (e.g. De Chantal et al. 2003, Hanssen 2003). Given their complexity and interrelated nature, it is critical to study multiple factors simultaneously to parse out which are most important within the particular regeneration context. Therefore, our approach was to analyze their combined and relative effects within a same model-based framework. Moreover, we examine the effects of various factors on regeneration by spatial gradients, i.e. each observation point's relative distance to the gap edge, paired with each gap's surrounding stand density to quantify the intensity of the competition-related components of

these gradients. Working with spatial distance-based gradients rather than gap sizes (e.g., large vs. small) enables users to apply the knowledge gained about the factors themselves for subsequent interpolation in terms of gap size.

The objectives of this study were to:

- simultaneously assess the effects of various gap characteristics and patterns of understory vegetation on the natural regeneration dynamics of Norway spruce (*Picea abies* (L.) Karst.) and birch species (*Betula pendula* Roth., *Betula pubescens* Ehrh.) 4–5 growing seasons post-harvest across harvested gaps;
- outline the most significant factors affecting the success of early regeneration for Norway spruce and birch;
- point to management actions which could facilitate natural tree regeneration in forest gaps under comparable conditions.

Materials and methods

Study area

This research was carried out in the Isojärvi experimental forest area in Southern Finland, which has been designated for research and development purposes under the DISTDYN project (Koivula et al. 2014). The experimental area is situated near the town of Jämsä at 61°40'N, 25°00'E, and covers an area of 689ha. It is managed according to the principles of Natural Disturbance Emulation (Attiwill 1994, Bergeron et al. 2002, Long 2009); please see Kuuluvainen and Aakala (2011) for typical natural forest dynamics in this region, and Koivula et al. (2014) for their application in the DISTDYN project.

Four different harvesting treatments are applied in the DISTDYN forests, of which “gap felling” and “partial felling” were relevant for this study. They involve harvesting small irregular clearcut gaps with areas of ca. 0.1–0.5 hectares and diameters of approximately 10–60m with 10–50m wide unharvested (residual) forest buffers in between (Fig. 1). In the Isojärvi experimental forest area, gap and partial felling was carried out in 40 stands during January and February of 2010 and 2011. Stand areas vary between 0.5 and 8.9 hectares and each harvested stand contains 1–7 gaps (making up 20–33% of the total stand area), depending on the availability of stand area, establishing a total of 86 gaps. The first harvesting round at Isojärvi failed to produce the very smallest gap sizes prescribed in terms of “gap felling”, and the final diameter range was 30–60m (vs. the intended range of 10–60m). As a result, the two treatment types produced rather similar harvesting results and were therefore merged and referred to as “gaps” in this study. Due to the winter conditions with almost constant subzero air temperatures and abundant snow cover present throughout, soil disturbance from harvesting was minimal.

The predominant forest site types in the Isojärvi area are the submesic *Myrtillus* type and the mesic *Oxalis-Myrtillus* type (Cajander 1909). 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). Norway spruce and birch make up the primary commercial species on the mesic and submesic sites at Isojärvi. However, as a legacy of the silvicultural preference for Scots pine until the 1980s, many pine stands are still present today on sites considered too fertile for the species. The current tendency in Finland today is to facilitate the conversion of these stands back to Norway spruce and birch. The understory vegetation is dominated by dwarf shrubs (e.g., *Vaccinium myrtillus*, and *Vaccinium vitis-idaea*), herbs, grasses/sedges, ferns, mosses and lichens.

Sampling and measurements

The data was acquired through measurements across harvested gaps located throughout different forest stands. Forest stands and gaps were chosen for this study according to a number of criteria. This study's stands were selected among the 15 stands where permanent stand development and tree regeneration monitoring plots had been established under DISTDYN (in 2010–2011 after “gap” or “partial” felling, as denoted by Koivula et al. 2014). Within this set of stands, we only included those on MT (*Myrtillus* type) or OMT (*Oxalis-Myrtillus* type) sites, leaving out the less fertile stands not suitable for Norway spruce or birch regeneration. Furthermore, we restricted sampling to gaps in the central portions of the stands to avoid external influences. Finally, only gaps not treated with site preparation were included in this study. One or two gaps were sampled

from each of the stands in this subset of suitable gaps. If several gaps met the above-mentioned criteria in a given stand, the gaps to be sampled were selected randomly among the subset. In total, eighteen harvested gaps were selected across thirteen forest stands, ranging in size from 0.10–0.36 hectares (mean area of 0.19ha, median area of 0.18ha).

Measurements were performed during the late summer of 2014. Baselines were established in each gap, with East-West and North-South orientations (Fig. 2). In gaps with diameters <40m, one baseline of each orientation was established, each spanning the whole interior of the gap (as is seen in Fig. 2). In gaps with diameters >40m, two baselines of each orientation were established, each extending approximately 20m into the gap interior from the gap edge. The gap edge was defined as the point where the baseline crossed the imaginary line that connected the bases of the two nearest trees, as per Runkle (1981).

Centered on the baselines, 1m wide sampling strips were established for measuring seedlings, understory vegetation and microsite types (Fig. 2). These were assessed on square plots (quadrats), each measuring 1m² (1m x 1m), at 2m intervals along the sampling strips. On these measurement plots, all Norway spruce and birch (*B. pendula* and *B. pubescens*) seedlings (≤5m) were counted. Each of these seedlings were assessed to determine whether they had emerged before (i.e., advance regeneration), or after the gap harvesting treatment. Recently emerged seedlings (“germinants”, less than one growing season old) were counted separately, as a subset of the seedlings which emerged after gap harvesting.

On these same plots, understory vegetation and microsite types were assessed by percent cover for several key groups, and the dominant microtopography (flat, mound, depression, slope) was recorded. The percentage covers were visually estimated by classes of 0.1% increments from 0–1%, and of 1% increments (1%, 2%, 3%, etc.) above 1%. Understory vegetation was assessed by

species groups, and 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*, which were trees), 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. Microsite type groups included: covered stone (by up to approximately 10cm of moss, humus, or soil), bare stone, logs (≥ 7 cm diameter), bases of standing trees, bases of stumps, decaying 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. There were 876 of these plots in total, and therefore 876 observations for all seedling, understory vegetation, microtopography, and microsite type variables.

Also centered on these baselines, 21m wide sampling strips were established for measuring trees (Fig. 2). These strips extended 10m beyond all of the seedling/vegetation/microsite sampling strips into the residual stand. For all standing trees on these sampling strips which were ≥ 5 m in height, the coordinates and diameter at breast height (1.3m) were recorded.

Statistical analyses

Mean values and standard deviations for the number of seedlings per m^2 (seedling density) and the percent covers of understory vegetation and microsites by groups were computed at each sampled distance from the gap edge, as well as for each strip orientation and microtopography type. Since the distributions of seedling counts and percent covers were severely non-normal, the

statistical significance of the differences between strip orientations and microtopography types was assessed by the non-parametric Kruskal-Wallis one-way analysis of variance test based on ranks. Where significant differences were found, pairwise comparisons between strip orientations or microtopography types were computed using Tukey's post-hoc test. These analyses were conducted separately for sample plots in the interior of the gaps and for those in the residual stand.

Generalized additive models (GAMs; Wood 2006) were developed to describe the relationships between the mean density of seedlings that emerged after harvest and the available explanatory variables. Given the often spatially complex nature of gap environments, the benefit of using GAMs is that they can uncover the non-linear effects of the explanatory variables (e.g., Robinson et al. 2011). In this study, nonparametric response functions were fitted to continuous predictors if the estimated degrees of freedom were greater than one. The number of seedlings per plot (seedling densities) were assumed to follow a negative binomial distribution, with mean values determined by the explanatory variables through the logarithmic link function.

The final models were found using backward stepwise regression, starting from the full model with all available explanatory variables (basal area, distance from gap edge, position in the gap, topography, as well as all assessed microsite types and understory vegetation groups). In each step, the current model was compared to all reduced models obtained by dropping one covariate according to the following criteria. In cases where several covariates were insignificant according to the ANOVA tests, the first criterion for selecting the one to eliminate was collinearity with significant covariates. If no statistically significant collinearities were found, then the covariate with the highest p-value was eliminated. This process continued until all covariates included in the model were statistically significant ($p < 0.05$). Note that pairs of

213 collinear predictors could thus remain in the final model, if they both were significant even when
214 the other was included. AIC scores were also used as a tool to assess the removal of covariate
215 terms at each step of the modeling process. The reduced model was confirmed as an
216 improvement on the full model if it also produced a lower AIC score by >2 . This process aimed
217 to produce a final model that included the smallest possible number of covariates while
218 producing the lowest AIC score and the highest possible deviance explained. For birch however,
219 we considered the factor type variable of position in the gap as well as the basal area of the edge
220 stand to be key attributes in this context, and therefore they were retained in the models
221 regardless of their final p-values and AIC scores (producing models with AIC scores higher only
222 by <2). It should be noted that when basal area was removed from the birch seedling model,
223 dwarf shrubs produced a significant p-value. The relative importance of the continuous
224 predictors in the final models was assessed by computing the decrease in 'Deviance explained'
225 resulting from dropping each predictor in turn from the full model (metric 'last' in Grömping
226 2006). All analyses were carried out in the R environment, version 3.1.2 (R Core Team 2014),
227 with package mgcv (Wood 2011) applied for GAM modelling.

228

Results

Observed seedling density

The mean seedling density per m^2 within the gaps was 20.36 for Norway spruce and 6.82 for birch species. Of the spruces, 62% were germinants (with an age of one growing season or less), 27% were seedlings that had emerged after harvesting and were older than one growing season, and 11% were advance regeneration that had existed prior to harvesting. These respective values for birch were 29%, 46%, and 25%. In the residual edge forests there were much fewer birch seedlings than inside the gaps (2.4 per m^2 on average), but almost as many spruces (19.6 per m^2 on average). Mean values of the studied variables for all plots combined, i.e. inside the gap and residual forest, are presented in Table 1. The greatest seedling density occurred inside the gaps, in the 5–10m zone for Norway spruce and in the 0–10m zone for birch species (Fig 3). 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 was high, 81% for birch species and 54% for spruce.

Some significant differences among the cardinal positions of the plots (“strip orientations”) and the microtopography types were found, but these varied by species and according to whether the plots were located within the gaps or in the residual forest stand (Tables 2 and 3). Inside the gaps, northern gap positions supported significantly fewer birch seedlings than the other gap positions; in the residual edge forests, western gap positions hosted the greatest density of spruce seedlings than the other gap positions. Among the microtopography types, depressions hosted more spruce seedlings than the other types inside the gaps (Tables 2 and 3).

251

252 *Observed vegetation cover*

253 The 0–15m zone inside the gaps supported the greatest number of different species groups (Fig
254 4). The edge zone in the residual edge forests favored dwarf shrubs and mosses. Gap centers
255 (~15m+) promoted grasses, shrubs, and herbs, creating a prolific and highly competitive
256 environment. Inside the gaps, northern gap positions were associated with a greater cover of
257 dwarf shrubs and grasses (Tables 2 and 3). In the residual edge forests, southern positions were
258 associated with a greater cover of grasses and herbs, and the eastern positions with a greater
259 cover of mosses.

260 There were a few significant differences in vegetation cover among the microtopography types
261 in the gap interior (Tables 2 and 3). The cover of shrubs was lower in depressions, while mosses
262 had greater covers on mounds, and grasses had greater covers on flat and sloped
263 microtopographies.

264

265 *Seedling density as a function of multiple interrelated factors*

266 According to the final GAM model for Norway spruce (Eq. 1 and Table 4), seedling density was
267 negatively related to the percent cover of shrubs, dwarf shrubs, grasses, and covered stones, and
268 positively related to basal area. The relationship with distance and herbs was a bit more complex
269 (Fig. 5). Among the continuous predictors, grasses was the most important. However, distance,
270 shrubs, and dwarf shrubs were almost as important. This model also indicated that the greatest
271 density of Norway spruce seedlings occurred in depressions.

272 The final model for the number of Norway spruce seedlings per m² that emerged after harvest,
 273 $E(N_S)$, was

$$\begin{aligned}
 \text{(Eq. 1)} \quad \log(E(N_S)) = & \beta_{\text{Microtopo}} + f_D(\text{Distance}) + f_S(\text{Shrubs}) \\
 & + f_{DS}(\text{Dwarf shrubs}) + f_H(\text{Herbs}) + f_G(\text{Grasses}) \\
 & + f_{CS}(\text{Covered stone}) + f_{BA}(\text{Basal area}),
 \end{aligned}$$

277 where the class-specific intercepts $\beta_{\text{Microtopo}}$ are obtained from the ‘Estimate’ column of Table 4
 278 so that β_{Flat} is the ‘Intercept’ and $\beta_{\text{Microtopo}}$ of any other microtopography class is the sum of the
 279 ‘Intercept’ and the ‘Estimate’ value of that class. The form of the response functions (f)
 280 estimated for the other significant predictors can be seen in Fig. 5.

281 According to the final GAM model for birch species (Eq. 2 and Table 5), seedling density was
 282 negatively related to the percent covers of grasses and dwarf shrubs, and only slightly positively
 283 related to basal area (Fig. 6). The relationship with distance, young stumps and decaying stumps
 284 was a bit more complex. The lowest densities of birch seedlings occurred in northern gap
 285 positions. Position in the gap was also found to influence the effect of distance. Therefore,
 286 separate responses to functions of distance ($f_{D,S}$) were estimated for each strip orientation (S).
 287 Distance was by far the most important predictor.

The final model for the number of birch seedlings per m² that emerged after harvest, $E(N_B)$, was

(Eq. 2)

$$\log(E(N_B)) = \beta_{\text{Strip orientation}} + f_{D,S}(\text{Distance})$$
$$+ f_G(\text{Grasses}) + f_{DS}(\text{Dwarf shrubs}) + f_{YS}(\text{Young stumps})$$
$$+ f_{DS}(\text{Decaying stumps}) + f_{BA}(\text{Basal area})$$

where the parameter values $\beta_{\text{Strip orientation}}$ for the different strip orientations are obtained from the ‘Estimate’ column of Table 5, and the form of the response functions (f) estimated for the other significant predictors in the eastern orientation can be seen in Fig. 6. 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.

Discussion

Modeling approach

Generalized Additive Models (GAM) were applied to simultaneously assess the relative effects of various gap characteristics and patterns of understory vegetation on the natural regeneration of Norway spruce and birch. They proved useful in uncovering the complex relationships observed in this study. However, the flexibility of GAMs, in combination with the large inherent variability in seedling counts on the small plots, can result in an overestimation of the complexity of relationships between variables and therefore somewhat unrealistic response curves. This is a feature that GAM users need to be aware of at all stages of its application.

Gradients by distance from the gap edge

The strongest factor controlling seedling density for both spruce and especially birch was the vicinity to the residual forest (the gap edge). Few seedlings had emerged in the residual forest stand; from the edge, seedling density increased towards the gap interior, peaked, then started to wane in the innermost gap regions. Additionally, GAM analyses revealed that greater residual edge stand basal areas resulted in greater seedling densities overall. These findings can be explained by two basic factors. First, competition from trees in the edge stand tends to limit the proliferation of light-demanding understory vegetation in its vicinity, facilitating a better emergence and survival of seedlings of the relatively more shade-tolerant spruce in inner-edge gap regions. Second, with increasing distance from the gap edge towards the gap center, the strong levels of competition exerted by prolific shrubs, dwarf shrubs, grasses and herbs on both above- and below-ground resources hinders seedling growth (Jäderlund et al. 1997, Bell et al.

2000, Hanssen 2003, Picon-Cochard et al. 2006), and acts as a physical impediment to seedling germination and the growth of smaller seedlings (for a broader discussion of these mechanisms, see Royo and Carson 2006).

One of the possible explanations for the distance-related pattern could be that seed rain from adult trees typically diminishes with increasing distance. However, the studies by Valkonen et al. (2011) and Valkonen and Siitonen (2016) have confirmed that seed dispersal distance is not an important factor on such small harvest areas for any of the major forest tree species covered by this study, confirming the conclusions of fundamental seed crop research (Heikinheimo 1937, Lehto 1956, Perala and Alm 1990).

An optimal distance for seedlings was encountered at about 5–10m from the gap edge inside the gap for spruce, and at about 5m for birch. With increasing distance from the gap edge the seedling densities tended to decrease, again likely due to the greater levels of competition from understory vegetation (especially from grasses, shrubs and herbs). The findings for spruce are in line with previous observations (Dai 1996, Burton 2002, Hanssen 2003, Valkonen et al. 2011).

As for birch, there is very little relevant previous information available. Nevertheless, also having studied the early regeneration of birch seedlings (within 5 years after harvest), Huth and Wagner (2006) similarly found very few birch seedlings in the central gap positions, explained by high levels of competition with grasses there. In slight contrast to our results, Valkonen et al. (2011) studied birch regeneration 10 years after harvest (twice as long as the regeneration period of this study) in 40m × 40m gaps, and found that the number of birch seedlings steadily increased from the gap edge towards the gap center. It can therefore be speculated that in the early regeneration phases of birch seedlings, the positive influence of potential light resources in the central gap positions is outweighed by the negative pressures of competition from dense

understory vegetation. In the later regeneration phases, however, the spatial patterns of successful seedling regeneration may more closely reflect the availability of light resources across the gap.

Position in the gap and microtopography

Variation in the abundance and composition of understory vegetation, as well as the gradient in distance from gap edge affected the observed natural tree regeneration. The cardinal position of the sample plots (with respect to the gap midpoint) influenced both the seedling density and the abundance of understory vegetation in variable ways. Some patterns and correlations were somewhat vague and hard to interpret unambiguously. However, some rather obvious patterns are worth mentioning. The greater spruce seedling densities observed in the western portions of the residual stand were likely due to the significantly lower herb cover observed there. Northern gap positions hosted low densities of birch seedlings. This result was somewhat unexpected, because birch species have a very low shade tolerance and in these latitudes the northern gap positions would presumably favour their exposure to light (Canham et al. 1990). However, Friesen and Michaels (2010) showed that the light-demanding Scots pine similarly did not generally benefit from the greater exposure to light in northern gap positions, signaling that other factors play a greater role in its regeneration. Similarly, other studies have reported a shift in the composition of understory vegetation towards the northern gap regions (Fahey and Puettmann 2008, Friesen and Michaels 2010).

In terms of microtopography, the greatest density of Norway spruce seedlings was observed in depressions, a finding that is in line with the results of several other studies (Hanssen 2003,

Kuuluvainen and Kalmari 2003, Diaci et al. 2005). This can be explained in part by the fact that depressions had significantly lower covers of shrubs and grasses. From small to moderate covers, microsites of covered stones promoted higher than average Norway spruce seedling densities, but this effect became negative with greater coverage. Both young and decaying stumps/logs were favorable microsites for birch seedlings, as found in previous studies by Liu and Hytteborn (1991), Grenfell et al. (2011), and Robert et al. (2012). However, in this study the effect was unimodal, peaking at 10–15 % cover, then waning with greater coverage.

Limitations of the study

First, seed crops in the area for the study period (2010–2015) can be described as having been average for birch but slightly more abundant than average for Norway spruce, which had three modestly abundant crops (in 2011, 2013, and 2015) alternating with poor crops (2010, 2012, and 2014) (personal communication, Tatu Hokkanen, Natural Resources Institute Finland, Luke).

Second, the observed microsites, edge effects, and patterns of understory vegetation across the gap environment will no doubt change as the gap ages. As a result, features that currently promote high numbers of seedlings will not necessarily support the most successful regeneration over time, and vice versa.

Conclusions

Our results suggest adequate potential for natural regeneration in harvested gaps under similar conditions if carried out with attention to several factors which may impede or promote natural regeneration. The emergence of spruce and birch seedlings seems abundant within the 0–15m

zone inside the gap. However, the inner gap region beyond 15m from the edge was characterized by limited seedling establishment, likely owing to the high levels of competition with understory vegetation. As a result, we recommend that harvested gap diameters should not exceed 40m in order to minimize the proliferation of competitive understory vegetation and to favor successful initial seedling establishment on mesic and submesic sites in Southern Finland. While these small gap sizes would be instrumental in promoting early seedling establishment, further expansion of the gaps through subsequent silvicultural interventions will likely be needed in order to provide established seedlings with greater access to resource (e.g., light) and to promote successful long-term regeneration.

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References

- Attiwill, P. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* 63(2-3): 247–300. doi: 10.1016/0378-1127(94)90114-7.
- Bell, F.W., Ter-Mikaelian, M.T., and 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(5): 790–800. doi:10.1139/x00-004.
- Bergeron, Y., Leduc, A., Harvey, B., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable forest management of the Canadian boreal forest. *Silva Fennica* 36: 81–95.
- Burton, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. *Silva Fennica* 36(1): 329–352. doi:10.14214/sf.566.
- Cajander, A.K. 1909. Über Waldtypen [Forest site types]. *Acta Forestalia Fennica* 1: 1–175.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20(5): 620–631. doi:10.1139/x90-084.
- 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(1–3): 187–197. doi:10.1016/0378-1127(96)03734-6.
- De Chantal, M., Leinonen, K., Kuuluvainen, T., and 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(1–3): 321–336. doi:10.1016/s0378-1127(02)00273-6.

Diaci, J., Pisek, R., and Boncina, A. 2005. Regeneration in experimental gaps of subalpine *Picea abies* forest in the Slovenian Alps. *European Journal of Forest Research* 124(1): 29–36. doi:10.1007/s10342-005-0057-7.

Domke, G.M., Caspersen, J.P., and Jones, T.A. 2007. Light attenuation following selection harvesting in northern hardwood forests. *Forest Ecology and Management* 239(1–3): 182–190. doi:10.1016/j.foreco.2006.12.006.

Fahey, R.T., and Puettmann, K.J. 2008. Patterns in spatial extent of gap influence on understory plant communities. *Forest Ecology and Management* 255(7): 2801–2810. doi:10.1016/j.foreco.2008.01.053.

Friesen, C., and Michaels, N. 2010. Effects of Incorporating Gaps into Commercial Thinning Prescriptions: Best Available Science. Central Cascades Adaptive Management Partnership (CCAMP). Available from <http://ecoshare.info/projects/central-cascade-adaptive-management-partnership/synthesis-papers-tools/> [accessed 10 January 2014].

Grenfell, R., Aakala, T., and 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(5): 1093–1110. doi:10.14214/sf.89.

Grömping, U. 2006. Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software* 17(1): 1–27. doi:10.18637/jss.v017.i01.

- Grushecky, S.T., and Fajvan, M.A. 1999. Comparison of hardwood stand structure after partial harvesting using intensive canopy maps and geostatistical techniques. *Forest Ecology and Management* 114(2–3): 421–432. doi:10.1016/S0378-1127(98)00372-7.
- Halpern, C.B., McKenzie, D., Evans, S.A., and Maguire, D.A. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecological Applications* 15(1): 175–195. doi:10.1890/03-6000.
- Hanssen, K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. *Forest Ecology and Management* 180(1–3): 199–213. doi:10.1016/s0378-1127(02)00610-2.
- Heikinheimo, O. 1937. Metsäpuiden siementämiskyvystä II. Referat: Über die Besamungsfähigkeit der Waldbäume II. [Seed production capacity of forest trees]. *Communicationes Instituti Forestalis Fenniae* 24(4): 67. Finnish with German summary.
- Hill, S.B., Mallik, A.U., and 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(8): 1942–1951. doi:10.1139/x05-126.
- Huth, F., and 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(1-3): 314–324. doi:10.1016/j.foreco.2006.04.010.
- Koivula, M., Kuuluvainen, T., Hallman, E., Kouki, J., Siitonen, J., and 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(6): 579–592. doi:10.1080/02827581.2014.938110.

- 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. Available from <http://www.jstor.org/stable/23735497> [accessed 4 February 2014].
- Kuuluvainen, T., and Aakala, T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica* 45: 823–841.
- Kuuluvainen, T., and 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. Available from <http://www.jstor.org/stable/23726798> [accessed 20 March 2014].
- Lehto, J. 1956. Tutkimuksia männyn luontaisesta uudistumisesta Etelä-Suomen kangasmailla. Summary: Studies on the natural reproduction of Scots pine on the upland soils of Southern Finland. *Acta Forestalia Fennica* 66(2) 106.
- Liu, Q., and Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *Journal of Vegetation Science* 2(3): 391–402. doi:10.2307/3235932.
- Long, J. 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. *Forest Ecology and Management* 257: 1868–1873.
- Palmer, M.W., and Dixon, P.M. 1990. Small-Scale Environmental Heterogeneity and the Analysis of Species Distributions along Gradients. *Journal of Vegetation Science* 1(1): 57–65. doi:10.2307/3236053.

Perala D., and Alm, A. 1990. Regeneration silviculture of birch: a review. *Forest Ecology and Management* 32(1): 39–77.

Picon-Cochard, C., Coll, L., and 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(3): 373–383.
doi:10.1007/s00442-006-0379-2.

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

Raymond, P., Munson, A.D., Ruel, J.-C., and Coates, K.D. 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood - white pine stands. *Canadian Journal of Forest Research* 36: 639–651.

Robert, E., Brais, S., Harvey, B.D., and Greene, D. 2012. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. *Canadian Journal of Forest Research* 42(8): 1446–1455. doi:10.1139/x2012-085.

Robinson, A.P., Lane, S.E., and Thérien, G. 2011. Fitting forestry models using generalized additive models: a taper model example. *Canadian Journal of Forest Research* 41: 1909–1916. doi: <https://doi.org/10.1139/x11-095>.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345–1362.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041–1051. doi:10.2307/1937003.

Stewart, K.J., and Mallik, A.U. 2006. Bryophyte responses to microclimatic edge effects across riparian buffers. *Ecological Applications* 16(4): 1474–1486. doi:10.1890/1051-0761(2006)016[1474:brtmee]2.0.co;2.

Tonteri, T. 1994. Species richness of boreal understorey forest vegetation in relation to site type and successional factors. *Annales Zoologici Fennici* 31: 53–60. Available from http://www.jstor.org/stable/23735498?seq=1#page_scan_tab_contents [accessed 4 February 2014].

Valkonen, S., Koskinen, K., Mäkinen, J., and Vanha-Majamaa, I. 2011. Natural regeneration in patch clear-cutting in *Picea abies* stands in Southern Finland. *Scandinavian Journal of Forest Research* 26(6): 530–542. doi:10.1080/02827581.2011.611818.

Valkonen, S., and Siitonen, J. 2016. Tree regeneration in patch cutting in Norway spruce stands in northern Finland. *Scandinavian Journal of Forest Research* 31: 271–278.

Vanha-Majamaa, I., Shorohova, E., Kushnevskaya, H., and Jalonen, J. 2017. Resilience of understory vegetation after variable retention felling in boreal Norway spruce forests – A ten-year perspective. *Forest Ecology and Management* 393: 12–28.

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

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. doi:10.1111/j.1467-9868.2010.00749.x.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. *In A Systems Analysis of the Global Boreal Forest. Edited by G.B. Bonan.* Cambridge University Press, Cambridge, UK. pp. 85–125.

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Table 1. Overview of the study's variables at measurement 4-5 years after harvesting.

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

*Note: Basal area is given in $\text{m}^2 \text{ha}^{-1}$ at stand level, tree regeneration values in number of individuals m^{-2} , vegetation and microsite cover values in % at plot level.

Table 2. Statistical significance (*p*) of differences between strip orientations and microtopography types on the basis of Kruskal-Wallis one-way ANOVA. The analyses were conducted separately for sample plots in the interior of the gaps (*inside*) and for those in the residual forest stand (*outside*). Significant *p* values < 0.05 in **bold**.

Factor	Position	Response								
		Seedling density m ⁻²				Cover, %				
		Norway spruce	Birch spp.	Shrubs	Dwarf shrubs	Herbs	Grasses	Ferns	Mosses	Lichens
		<i>p</i>								
Strip orientation	<i>inside</i>	0.735	0.003	0.268	0.004	0.169	0.017	0.093	0.282	0.251
	<i>outside</i>	0.018	0.292	0.670	0.164	0.009	0.020	0.313	0.006	0.233
Micro- topography type	<i>inside</i>	0.011	0.391	0.012	0.134	0.297	0.001	0.596	0.047	0.092
	<i>outside</i>	0.576	0.026	0.410	0.189	0.232	0.690	0.081	0.354	0.834

Table 3. Mean value of the response variable for each strip orientation or microtopography type for those combinations of factor, position, and response where significant differences were reported in Table 2. The results of pairwise comparisons by Tukey's post-hoc test are indicated by lowercase letters following the mean values: if two values of the same row share a common letter, then they are not significantly different in a pairwise comparison.

Position	Response	Strip orientation			
		<i>N</i>	<i>E</i>	<i>S</i>	<i>W</i>
<i>inside</i>	<i>Birch spp.</i>	0.16a	0.62ac	0.94bc	1.04c
	<i>Dwarf shrubs</i>	12.77a	8.27b	8.97ab	6.28b
	<i>Grasses</i>	30.92a	19.62b	27.26ab	23.62ab
<i>outside</i>	<i>Norway spruce</i>	1.35a	1.50a	1.42a	3.42b
	<i>Herbs</i>	4.10ab	3.18ab	4.68a	3.05b
	<i>Grasses</i>	2.56a	3.42a	6.90b	2.44a
	<i>Mosses</i>	66.33a	77.41b	60.88a	70.01ab
Position	Response	Microtopography type			
		<i>Flat</i>	<i>Slope</i>	<i>Depression</i>	<i>Mound</i>
<i>inside</i>	<i>Norway spruce</i>	2.34a	1.03a	7.00b	1.62a
	<i>Shrubs</i>	14.03a	15.36a	5.86bc	13.06ac
	<i>Grasses</i>	28.54a	24.29a	11.89b	11.74b
	<i>Mosses</i>	32.57a	31.99a	35.41a	43.79a
<i>outside</i>	<i>Birch spp.</i>	0.21ab	0.25ab	0.00a	0.52b

Table 4. Summary of the GAM for the number of Norway spruce seedlings per m² which emerged after harvest.

Parametric coefficients*:				
	Estimate	Std. Error	z value	Pr(> z)
Intercept	0.08117	0.09923	0.818	0.41338
Microtopo _{Slope}	-0.45819	0.19991	-2.292	0.02191 *
Microtopo _{Depression}	1.08783	0.37806	2.877	0.00401 **
Microtopo _{Mound}	0.50308	0.24699	2.037	0.04166 *
Approximate significance of smooth terms:				
	edf [†]	Chi.sq	p-value	Relative importance, %
s(distance)	4.729	27.194	0.000122 ***	3.9
s(shrubs)	1.000	32.618	1.12e-08 ***	4.2
s(dwarf shrubs)	1.002	30.891	2.81e-08 ***	3.9
s(herbs)	3.579	11.526	0.028751 *	1.5
s(grasses)	2.854	46.215	2.32e-09 ***	5.9
s(covered stone)	1.000	20.321	6.56e-06 ***	2.5
s(basal area)	1.470	9.215	0.008566 **	1.0
Observations	876			
Deviance explained	22.8%			

* Estimates of the parametric coefficients: ‘Intercept’ is the mean value in the reference category Flat, whereas Microtopo_{Slope}, Microtopo_{Depression} and Microtopo_{Mound} are the difference between the Intercept and the mean of the Slope, Depression and Mound categories, respectively.

† Estimated degrees of freedom (edf) for the cubic spline smoothers; ranges from edf = 1 (the GAM estimates that a single slope parameter explains the relationship, i.e. it is linear) to edf = n–1 (the GAM estimates that a unique parameter is required to fit each observation, i.e. the relationship is highly non-linear).

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

Table 5. Summary of the GAM for the number of birch seedlings per m² which emerged after harvest.

Parametric coefficients*:				
	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(> z)</i>
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:				
	<i>edf</i> [†]	<i>Chi.sq</i>	<i>p-value</i>	<i>Relative importance, %</i>
s(distance): Strip _{North}	1.000	1.120	0.28994	14.3
s(distance): Strip _{East}	3.025	12.553	0.01190 *	
s(distance): Strip _{South}	3.507	13.585	0.01218 *	
s(distance): Strip _{West}	3.444	18.435	0.00143 **	
s(dwarf shrubs)	1.689	5.693	0.06500	1.4
s(grasses)	1.001	3.854	0.04983 *	0.8
s(young stumps)	1.176	11.822	0.00136 **	2.2
s(decayed stump)	2.646	13.689	0.00471 **	3.2
s(basal area)	1.000	1.636	0.20085	0.3
Observations	876			
Deviance explained	31.6%			

* Estimates of the parametric coefficients: 'Intercept' is the mean value in the reference category North, whereas Strip_{East}, Strip_{South} and Strip_{West} are the difference between the Intercept and the mean of the East, South and West categories, respectively.

† Estimated degrees of freedom (*edf*) for the cubic spline smoothers; ranges from *edf* = 1 (the GAM estimates that a single slope parameter explains the relationship, i.e. it is linear) to *edf* = *n*-1 (the GAM estimates that a unique parameter is required to fit each observation, i.e. the relationship is highly non-linear).

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

Figure captions

Figure 1. An example of harvesting in the 50% intermediate-scale disturbance block (here referred to as OH50% using Finnish terminology). Gaps are shown in red (“Pienaukko” in Finnish, as seen in the legend), and partial harvests in green (“Osittaushakkuu”); the light brown areas represent first commercial thinning (“Ensiharvennus”), and the dark brown represents thinning in the residual stand (“Välialueen harvennus”).

Figure 2. Experimental setup for gap analysis.

Figure 3. Mean seedling density in relation to gap edge (seen here as the dotted line).

Figure 4. Mean percent cover of species groups as a function of distance from gap edge (seen here as the dotted line).

Figure 5. Estimated seedling density (per m^2) for spruce which emerged after harvest as a function of GAM covariates, fixed for flat topography. Shaded bands indicate the 95% confidence intervals. *Distance* = distance of plot i from the gap edge (m); *Basal area* = basal area of the residual forest surrounding the gap of plot i ($\text{m}^2 \text{ ha}^{-1}$); *Shrubs*, *Dwarf shrubs*, *Herbs*, *Grasses* = percent cover of each species group on plot i (%); and *Covered stone* = percent cover of this microsite type on plot i (%).

Figure 6. Estimated seedling density (per m^2) for birch which emerged after harvest as a function of GAM covariates, fixed for an eastern strip orientation. Shaded bands indicate the 95% confidence intervals. *Strip* = orientation class of sampling strip of plot i (North, South, East, West); and *Young stumps*, *Decaying stumps* = percent cover of these microsite types on plot i (%); others are as explained in Fig. 5 caption.

Fig. 1.

Figure 1. An example of harvesting in the 50% intermediate-scale disturbance block (here referred to as OH50% using Finnish terminology). Gaps are shown in red (“Pienaukko” in Finnish, as seen in the legend) and partial harvests in green (“Osittauhakkuu”); the light brown areas represent first commercial thinning (“Ensiharvennus”), and the dark brown represents thinning in the residual stand (“Välialueen harvennus”).

Fig. 2.

Figure 2. Experimental setup for gap analysis.

Fig. 3.

Figure 3. Mean seedling density in relation to gap edge (seen here as the dotted line).

Fig. 4.

Figure 4. Mean percent cover of species groups as a function of distance from gap edge (seen here as the dotted line).

Fig.5.

Figure 5. Estimated seedling density (per m²) for spruce which emerged after harvest as a function of GAM covariates, fixed for flat topography. Shaded bands indicate the 95% confidence intervals. *Distance* = distance of plot *i* from the gap edge (m); *Basal area* = basal area of the residual forest surrounding the gap of plot *i* (m² ha⁻¹); *Shrubs*, *Dwarf shrubs*, *Herbs*, *Grasses* = percent cover of each floristic group on plot *i* (%); and *Covered stone* = percent cover of this microsite type on plot *i* (%).

Fig. 6.

Figure 6. Estimated seedling density (per m²) for birch which emerged after harvest as a function of GAM covariates, fixed for an eastern strip orientation. Shaded bands indicate the 95% confidence intervals. *Strip* = orientation class of sampling strip of plot *i* (North, South, East, West); and *Young stumps*, *Decaying stumps* = percent cover of these microsite types on plot *i* (%); others are as explained in Fig. 5 caption.