How Rocks Affect the Growth of Krummholz in the Mealy Mountains of Labrador

Honours Thesis by: Stephanie Daley
Supervisors: Karen Harper and Brian Starzomski

Introduction

Climate change has become a widely accepted phenomenon in the scientific world, and many studies seek to document its effects. In the Arctic, temperatures have generally been increasing more than in temperate zones (Balling et al.,1998; Griggs & Noguer, 2001), causing changes in subarctic and arctic ecosystems. The transitional zones between communities, which are referred to as ecotones, are particularly sensitive to change. The forest-tundra transition represents one such ecotone in which climate change has widely affected existing plant communities (Szeicz & MacDonald, 1995; Kullman, 2002; Danby and Hik, 2007; Meshinev, Apostolova, & Koleva, 2000).

While the structure of the forest-tundra ecotone can vary, it is generally characterized by a transition from closed canopy through open canopy forest, and then to a patchwork of forested and non-forested areas leading to the tundra zone (Apps et al., 1993). Trees within the forest-tundra ecotone can be distinguished by stunted growth forms which reflect limitations imposed by a harsh environment (Tranquillini, 1979). Limiting factors may include temperature, length of the growing season, harsh winds, browsing animals, drought, and genetic factors (Broll & Keplin, 2005; den Herder, Virtanen, & Roininen, 2008). Referred to as krummholz, this growth form often propagates by forming thick, layered mats rather than by adding height. By growing in this manner, trees can maintain a variety of genotypes in landscapes where sexual reproduction is often not possible until conditions are more favourable (Gamache et al., 2003).

The presence of rocks could alter the growth and establishment of krummholz in many ways. For example, rocks may create a favourable microclimate for plants, resulting in a sort of positive interaction that might be termed 'passive facilitation' (Nagy and Grabherr, 2009) Most studies of facilitative effects have been conducted amongst biotic (i.e., plant-plant) components, rather than abiotic components (i.e., rock-plant). While plants sometimes compete for resources, many studies have found that they can facilitate one another as well. This facilitation link has been particularly evident in stressful environments (Eranen & Kozlov, 2007; Callaway et al, 2002), where the stress–gradient hypothesis predicts that high abiotic stress conditions will lead to greater facilitation (Bertness & Callaway, 1994). Many arctic and subarctic studies have focused on this concept, and experimental approaches have found evidence to support this hypothesis (Le Roux and McGeoch, 2008; Eranen & Kozlov, 2008). A major hypothesis on the workings of these "nurse plants" focuses on the shelter benefits they provide. This aspect of facilitation is most relevant for the purpose of this thesis, as rocks are more likely to provide shelter benefits than nutritional benefits. The benefits of shelter have long been of interest in agricultural settings, and can have many effects on plant growth. Shelter belts are often planted to prevent erosion; however, they have also been shown to increase air temperature (Bergez and Dupraz, 2000), affect moisture distribution, (Frank and Willis, 1972), and decrease direct solar radiation (Bergez and Dupraz, 2000). Other subarctic research has found that wind protection is of great importance at the beginning of the growing season, when desiccation is a danger (Wilson, 1959). Shelter can affect snow dispersal as well, as it can create longer and deeper drifts that cover and protect plants; this is important, as some species rely heavily on snow cover for winter survival (Hadley and Smith, 1987; Carlsson and Callaghan, 1991). In particular, a study on krummholz found that snow cover was essential for maintaining moisture in needles and preventing cuticle abrasion, which in turn decreased the rate of needle mortality (Hadley and Smith, 1987).

A second hypothesis for nurse plant facilitation is that nutrients are generated and trapped by nurse plants, causing improved growth. While some studies have illustrated higher nutrient levels around nurse plants, shading and root competition still inhibited seedling growth (Walker, Thompson & Landau, 2001). Further, Valiente-Banuet et al. (1991) found that nitrogen levels were lower within clusters of plants than they were in bare areas, contradicting the nutrient-based theory. Overall, the weight of evidence seems to be against the notion of nutritional facilitation, as the competitive aspects of plants in close quarters seem to consistently outweigh the benefits of nutrition. However, these studies focus largely on desert ecosystems, so the possibility of alternate dynamics in the alpine tundra cannot be disregarded. Because rocks do not provide nutrients, investigating how rocks affect the growth of krummholz could be a step in isolating whether growth effects in nurse plants are due to nutrient enrichment or shelter.

The purpose of this thesis is to investigate how rocks affect the growth of coniferous krummholz of two species: Black Spruce (*Picea mariana*) and Balsam Fir (*Abies balsamea*). Specifically, I investigated: 1) whether krummholz are spatially aggregated around rocks; 2) whether krummholz size is correlated with proximity with rocks; 2) whether annual growth of fir stems changes with proximity to rocks; and 3) whether krummholz are more likely to be found on a particular side of the rocks.

I carried out an observational study which cannot be used to determine cause and effect. It can, however, show relationships between the krummholz and rocks. This knowledge can be used to infer what processes may be occurring, which is a valuable first step in understanding the facilitation or inhibition effects rocks may have on krummholz.

Methods

The Mealy Mountains of Labrador are located at 53.62˚N / 58.84˚W. The average annual precipitation in the area is over 2 m (Labrador Highland Research Group, 2007); snowfall is heavy in the winter, and snow cover persists on alpine peaks until the late summer months. The mean temperature in the month of July (for the years 2001-2006) was 13.2 degrees Celsius, while the January mean was -15.4 degrees Celsius. There were an estimated 688 growing degree days in that period (De Fields, 2009). The dominant tree species include black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), eastern larch (*Larix laricina*), and white spruce (*Picea glauca).* Krummholz are a major feature of the plant community and large rocks are a major physical feature of the landscape. Glacial movement has shaped the Mealys, and the valley used as a case study in this thesis had regions of undisrupted vegetation as well as regions littered with large rocks.

Data Collection

I established a 50 by 50 m plot in an area with a large number of rocks and krummholz. I then recorded the location of all krummholz, and all rocks taller than 40 cm and wider than 120 cm in the plot. Including only large rocks in my measurements served to keep the sample size manageable and excluded rocks that seemed unlikely to provide shelter benefits to krummholz. I measured the length, width, and height of each rock and each krummholz. In one part of the plot, individual krummholz could not be identified due to their high density. Since the area was homogenous black spruce, I measured the perimeter of the entire area. For 16 randomly selected fir krummholz, I measured the annual height growth increments on up to five upright stems (where present) within each krummholz. This measurement was only possible on the fir because of visible growth scars formed every year.

I set up an additional 30 by 100 m belt transect beside the plot to obtain further empirical data on the position and presence of krummholz in relation to rocks. Within the belt transect, I recorded the orientation of fir and black spruce krummholz in relation to rocks, noting the number of krummholz immediately (within 15 cm) east, west, north and south of present rocks.

Data Analysis

First, I plotted a map of all rocks and krummholz in the plot (Figure 1). Because I was unable to fully characterize the high density patch of black spruce during data collection, I made three maps which characterized this patch as either high density, medium density, or low density. The results presented in this paper are representative of the medium density point pattern, as results varied little when compared with the low density representation and the high density site with many small krummholz seemed unlikely.

I used a method of point pattern analysis called neighbourhood density function (NDF) in order to establish whether spatial patterns were present in the plot. NDF analyzes bands of space around variables at increments defined by the researcher, and compares the number of points found within that increment with the number that would be expected if the points were randomly distributed. I chose a band width interval of 2 m, as the large size of the rocks and krummholz in my plot made finer scales unlikely to provide a useful characterization. A 95% confidence interval was constructed for each increment based on 500 simulations of randomly distributed points (Perry, 2004). If there are more points present than would be expected in a random distribution, the rocks or krummholz are aggregated, whereas fewer points indicate a regularly spaced variable. The magnitude of difference between the confidence interval and the peaks and troughs illustrate the intensity of the pattern. NDF can be used in both univariate and bivariate analysis, and I used both in this study in order to examine the spatial relationships between all variables. Univariate analysis was used in comparing the position of rocks in relation to the other rocks in the plot, as well as how krummholz related to other krummholz. Bivariate analysis was used to illustrate how krummholz related to rocks, as well as to examine how fir related to rocks and how spruce related to rocks. All spatial pattern analysis was done with the Excel add-in called SpPack (Perry, 2004).

In order to look at whether distance from rocks influenced krummholz size, I used trigonometry to map end points of the long and short axis of all measured krummholz, creating an approximate representation of their size. I located the closest rock to the north west of each krummholz, plotted its size in the same manner and then measured the approximate shortest distance between the two variables. I used a nonparametric Spearman rank correlation coefficient to analyze whether there was relation between distance from sheltering rocks and height of living stems, height of dead stems, length, width, number of upright stems, and growth rate (fir only) of the associated krummholz.

To examine whether krummholz had a tendency to be located on a particular side of rocks, I simply looked at the number counted on each side of the rocks within the belt transect and added that to the number I counted on each side within the plot. I used these numbers to calculate the overall percentage of krummholz associated with a given side of a rock.

Results

The rocks in the plot were approximately 2 by 1.5 metres, with a height of about a metre. Fir measured an average of about 3 by 1.6 metres, with a height of 0.7 metres, and spruce were smaller on average, at 2.3 by 1.5 metres, with a height of about 0.6 metres (Table 1).

Univariate NDF Analysis of rocks revealed aggregation at intermediate distances, from 4 to 10 m, as well as at larger scales of 20 and 24 m (Figure 2). When both species of krummholz were analyzed together, the NDF revealed aggregation from 4 to 12 m. Krummholz were regularly distributed from 0 to 2 m, as well as at 20 m (Figure 3). Bivariate analysis of rocks and krummholz indicated positive association at distances of 4 to 6 m (Figure 4). Spruce aggregated around rocks at distances of 4 to18 m (Figure 5). Fir was positively correlated with rocks at distances of 2 to 6 m (Figure 6).

The Spearman's correlation between distance to the nearest upwind rock and height of the tallest living stem, height of the tallest dead stem, length, width, number of upright stems, and growth rate were not significant (Table 2).

Overall, krummholz that were directly associated with rocks (touching or within 15cm) were most commonly located east of rocks, with 31.5% of the recorded krummholz in this position. Their frequency of association on the other three sides ranged from 22.8% to 26.2%. Both species were found in this position most often, although fir was located north of rocks at the same frequency (33.9%). Spruce was least likely to be located north of rocks, found in this position only 15.6% of the time.

Discussion

Krummholz Spatial Pattern

Krummholz aggregation around rocks in the Mealys suggests that facilitation influences their placement. NDF analysis only indicates the distance between centre points, but based on the average size of both rocks and krummholz, the edges of rocks tend to be about 2-4 metres from the edges of krummholz. This indicates that krummholz tend to be quite close to associated rocks. Fir tended to be in closer proximity to rocks than spruce, with centres establishing at 2-6 metres as opposed to spruce's 4-18 metres. This may be a function of each species' tolerance for certain conditions, which may allow fir to establish more often in favourable microsites. In this instance, shade may be the main factor influencing placement, as both fir and spruce are very shade tolerant, but spruce are less tolerant of shade when they are seedlings (Fowells, 1965). Rocks may influence krummholz spatial pattern not only by facilitating their growth, but by displacing them as well. Rocks are aggregated at 4-10 metres, which encompasses the range at which krummholz aggregate around rocks. In other words, krummholz are establishing at distances where space is somewhat limited, which makes their establishment in these microsites even more significant. This is well illustrated when contrasting the centre right-hand side of the plot, where there is plenty of open space and very few krummholz, with the lower left-hand side of the plot, where space is limited by many rocks, yet and abundance of krummholz have established. Overall, this supports the idea that krummholz benefit from the presence of rocks.

Another study on an alpine treeline established a positive link between geomorphic landscape features and tree establishment and suggested that shelter benefits are the main mechanisms by which rocks facilitate alpine vegetation (Resler, 2006). Shelter can protect individual plants from harsh winds, trap seeds, moderate temperatures, influence soil moisture (Carlsson and Callaghan 1991), and stabilize soil (Anderson and Bliss, 1998). Studies on the benefits of shelter have found that windbreaks can lower wind speeds up to distances many times their height, and that porosity is a significant factor in windbreak effectiveness (Frank and Ruck, 2005; Bird et al, 1992). Rocks could be expected to have similar far-reaching effects; shelter benefits from some rocks in the Mealys that are a few metres high may extend to large areas. Former studies in the Mealys provide further support for the shelter hypothesis as they indicate that soil quality is not limiting the growth of plants in the area (Bell et al., 2008).

In addition to benefiting individual trees, Resler (2006) found that shelter contributed to a cycle of positive feedback wherein trees establish and facilitate further establishment. Trees can contribute shelter benefits in much the same way as rocks, and their spread may extend the areas where krummholz can establish. In some krummholz sampled in my plot, fir and spruce were mixed and intertwined, implying that competitive disadvantages of close proximity to other plants may be overcome by facilitation effects in some instances. If krummholz expansion leads to further krummholz establishment, some very large mats consisting of multiple individuals (and particularly the large dense patch of spruce which I had difficulty measuring) may have expanded in the plot due to cycles of positive feedback. Univariate NDF analysis supported this further, indicating positive interactions reflected by krummholz clustering around one another.

Resler's study also found that trees were more likely to establish on the leeward side of rocks, and the results of this study found that krummholz were more likely to be located to the east of rocks. Since the prevailing winds in the Mealys come from the Northwest, this may support the idea that krummholz are positioned in a manner that shelters them from prevailing winds. These results may have been influenced by the density of rocks in the plot, as many krummholz counted as being placed on different sides of multiple rocks. Also, as sampling was done, only four directions were accounted for. A broader study of a less dense rocky area may further clarify whether a tendency does exist to establish on the leeward side of rocks.

Relationship of Rocks to Growth

Krummholz stem height and annual growth were not affected by distance to rocks. While this appears to contradict the idea that shelter benefits are important, it may simply indicate that the shelter rocks provide becomes less important as krummholz grow. A study by Callaway (1998) suggested that facilitation was more important for grown trees than saplings, since saplings obtain shelter from snow cover in the winter. The trees in Callaway's study were not located in as harsh an environment as the Mealys however, and did not have the krummholz growth form. This may be the key to these contradictory results. Unlike upright growing trees, larger and taller krummholz tend to have more stems; this layering may eventually act as a shelter for central stems, allowing them to grow uninhibited by wind damage. Furthermore, the layered, relatively short mats of krummholz are much better at catching snow than an upright tree. At a certain point, the plant may effectively shelter itself. If this is the case, it would suggest that rocks are most essential in aiding krummholz at the establishment stage.

Treeline Change

Krummholz in the Mealy Mountains forest tundra may have established up to several hundred years ago. Spatial patterns therefore demonstrate past growth conditions. At present, seedlings are not establishing in the upper regions of the Mealys (Bell et al., 2008). The barriers to establishment are not well understood, but it is believed that availability of seeds may be a key issue (Bell et al, 2008). If altered climatic conditions cause favourable conditions for seed production, past patterns such as establishment and survival around rocks may determine how treeline expands. In the future, rocks may act as vectors of treeline expansion, allowing establishment of krummholz. Krummholz may then expand outward around rocks, both by growing new stems and by allowing establishment of new individuals.

In the lower altitudes of the same range, larch seedlings have been shown to aggregate in close proximity to nearby adults and other juveniles (De Fields, 2009). While this study did not include analysis on the effects of rocks, it is conceivable that larch may respond to rocks in the same way. Larch appear to be the only tree species still sexually reproducing in the open canopy of the Mealys, and their advancement may change community composition by moving into areas where they did not previously establish.

Conclusions and Implications

This study suggests that abiotic features may affect the spatial development of plant communities. In areas marked by extreme conditions, such as treeline communities, these abiotic features may be of particular importance in facilitating plant growth. At present, treeline movement in the Mealys is limited by the lack of sexual reproduction in the area. However, climate change may alter conditions in a manner which allows for advancement. If this occurs, past patterns of rock and krummholz facilitation may again come into play. Treeline change affects not only plant communities, but the animals which rely on them as well. Any expansion or regression of the krummholz population would affect the quantity and placement of habitat and food for these animals, which could lead to changes within their populations. As the Mealy Mountains will likely become a National Park very soon, knowledge about krummholz growth could be useful to Parks Canada decision makers as they make land and wildlife management decisions which account for the effects of climate change.

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Table 1. The number, average size, and standard deviation of rocks, spruce krummholz and fir krummholz measured within the plot.

Variable	Number	Average length (cm)	Standard deviation of length (cm)	Average width (cm)	Standard deviation of width (cm)	Average height (cm)	Standard deviation of height (cm)
Rocks	106	204	+/- 80.6	147	+/- 68.1	92	+/- 50.4
Fir krummholz	37	292	+/-155	160	+/- 83.7	68	+/- 41.2
Spruce krummholz	25 + 35 estimated in dense patch	230	+/- 93.1	148	+/- 86.7	63	+/- 33.9

Table 2. The p-value and Spearman's correlation co-efficient for various measures of krummholz size.

	Distance vs. annual growth	Distance vs. height of the tallest living stem	Distance vs. height of the tallest dead stem	Distance vs. number of Upright stems	Distance vs. Length	Distance vs. Width
Correlation	-0.146	0.088	0.173	0.148	-0.062	-0.175
P-value	0.303	0.269	0.139	0.132	0.320	0.091

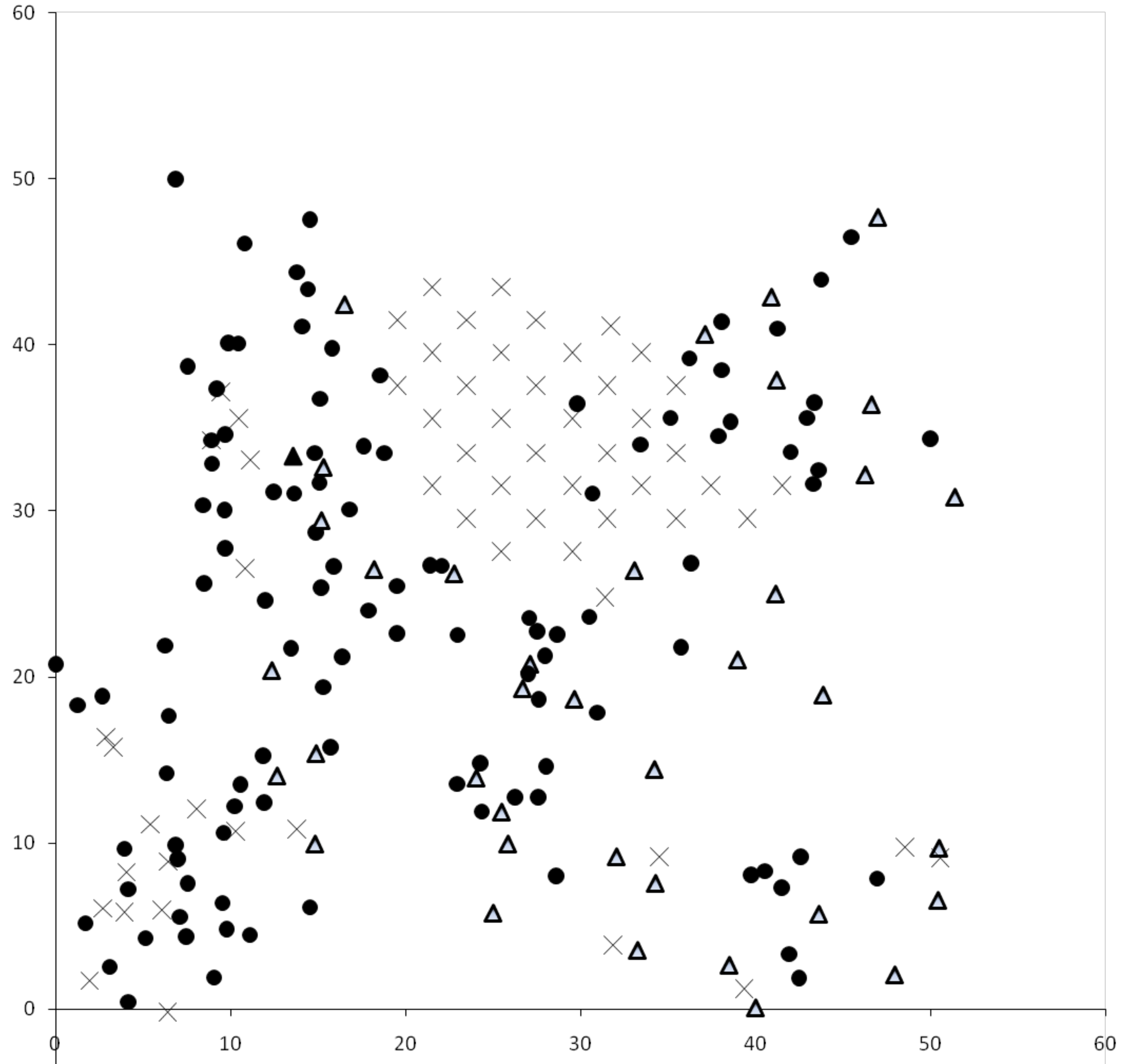

Figure 1. Map of rocks (circles), fir krummholz (triangles) and spruce krummholz (X's) within the plot. The axis units are in metres.

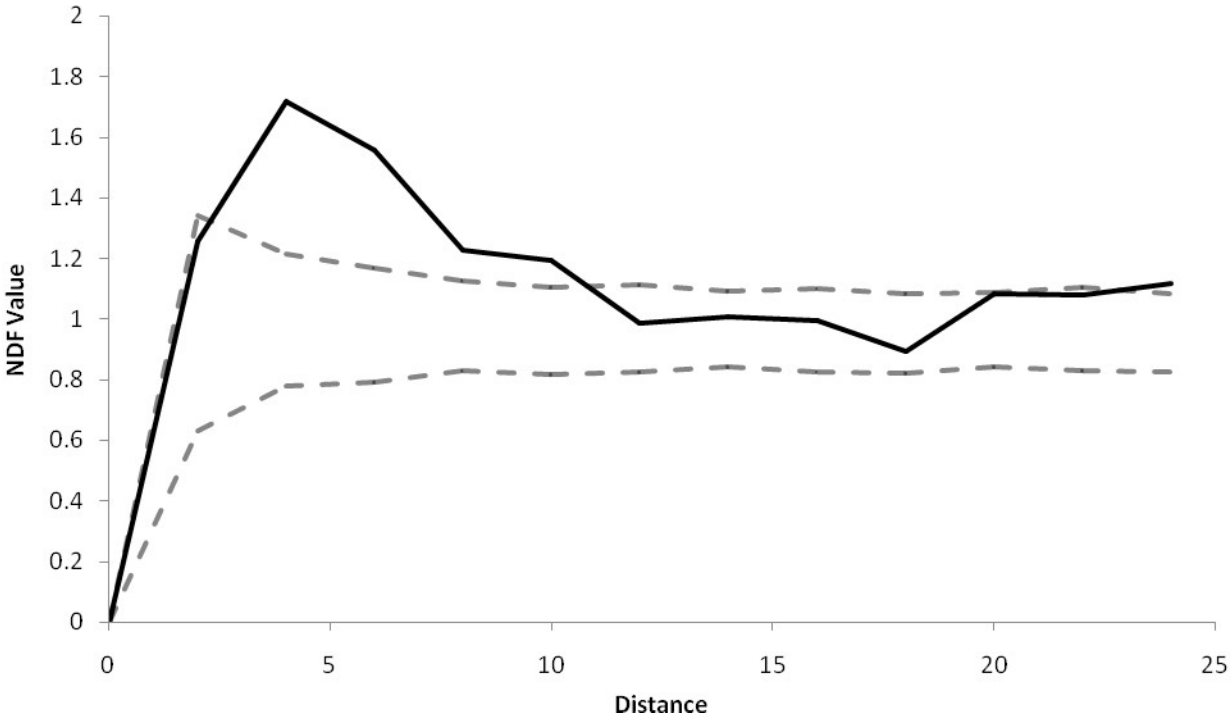

Figure 2. Univariate NDF analysis of all rocks in the plot. The dashed lines represent the 95% confidence interval, while the solid line represents the calculated NDF value.

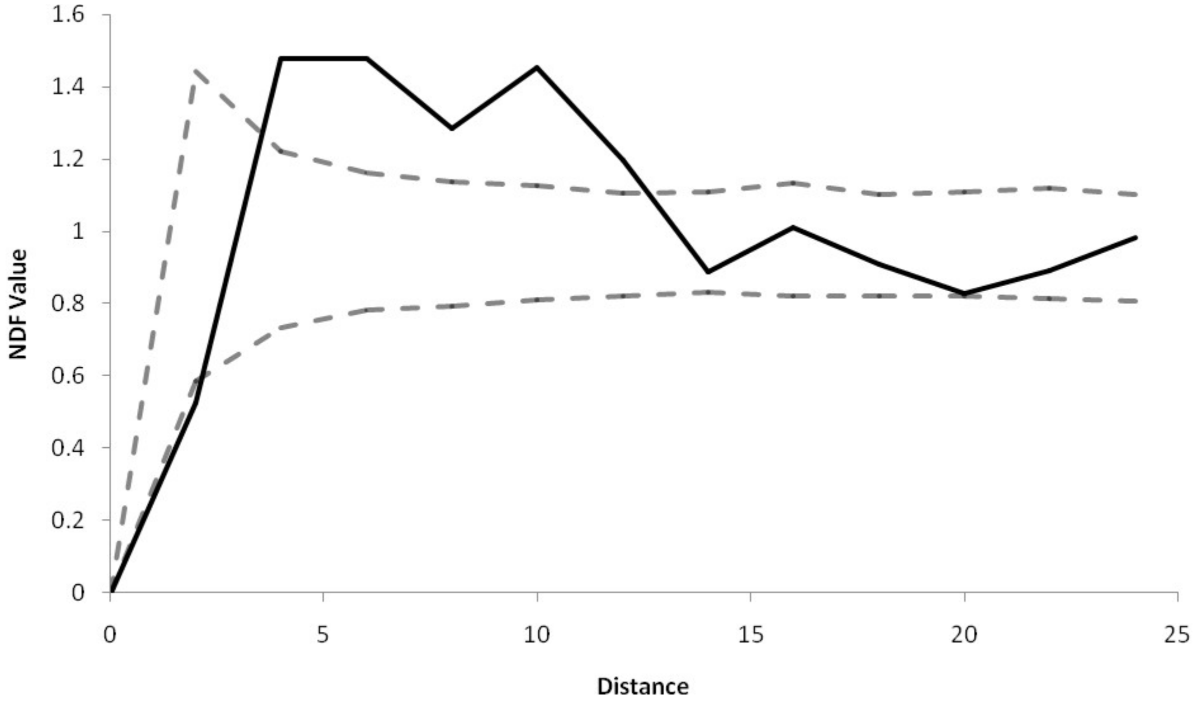

Figure 3. Univariate NDF analysis of all krummholz in the plot. The dashed lines represent the 95% confidence interval, while the solid line represents the calculated NDF value.

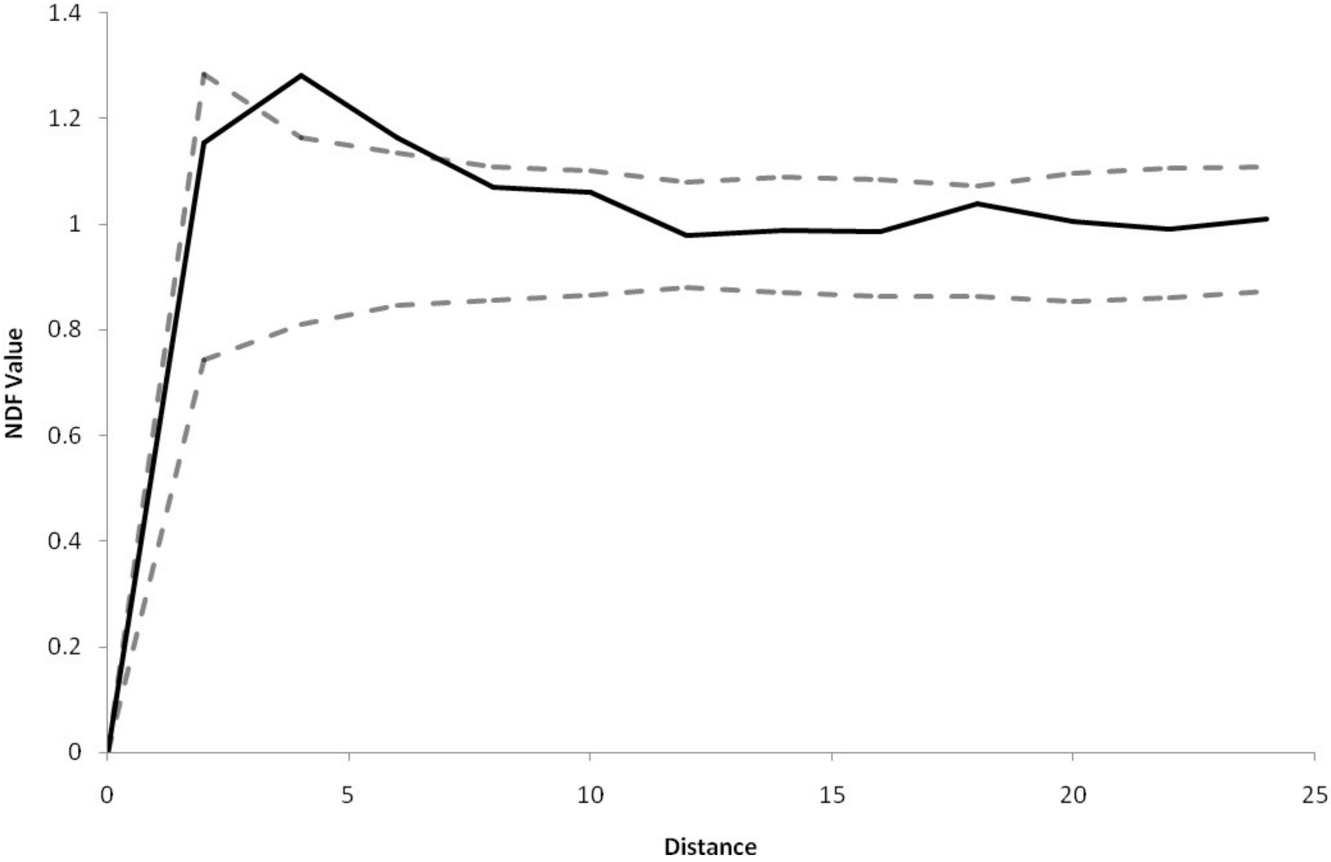

Figure 4. Bivariate NDF analysis of the relation of krummholz to rocks. The dashed lines represent a 95% confidence interval, while the solid line represents the calculated NDF value.

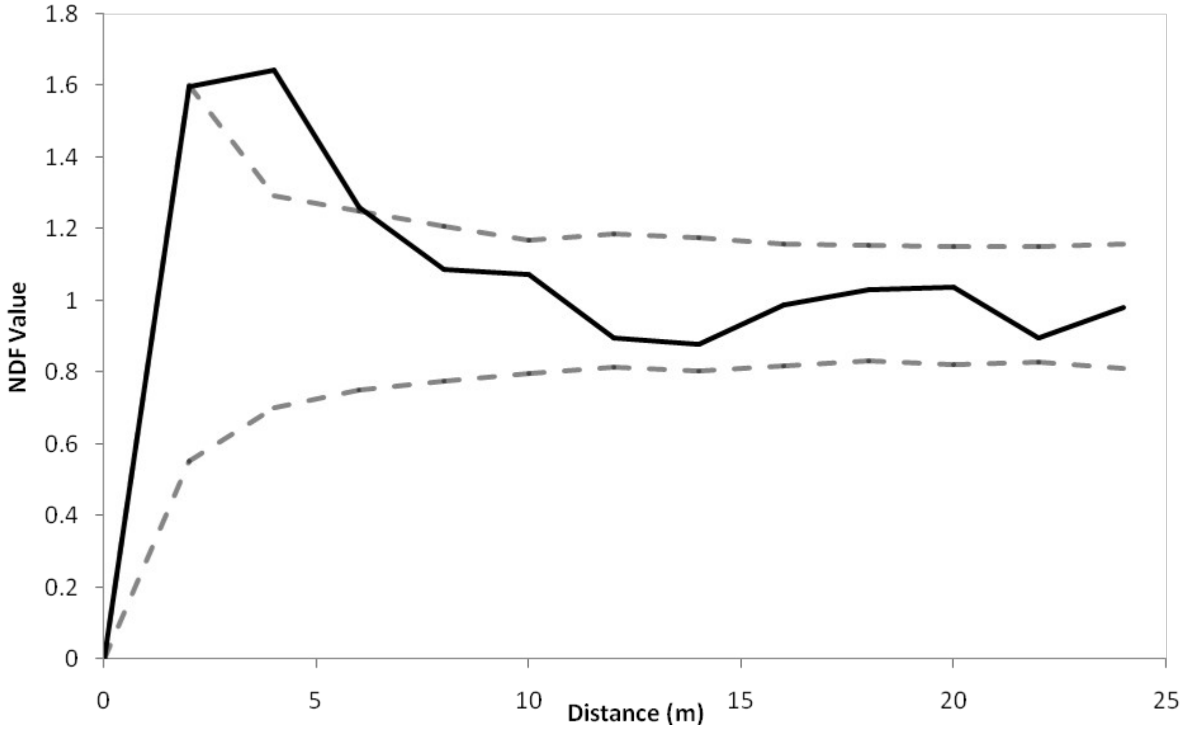

Figure 5. Bivariate analysis of the point patterns of fir and rocks. The dashed lines represent a 95% confidence interval, while the solid line represents the calculated NDF value.

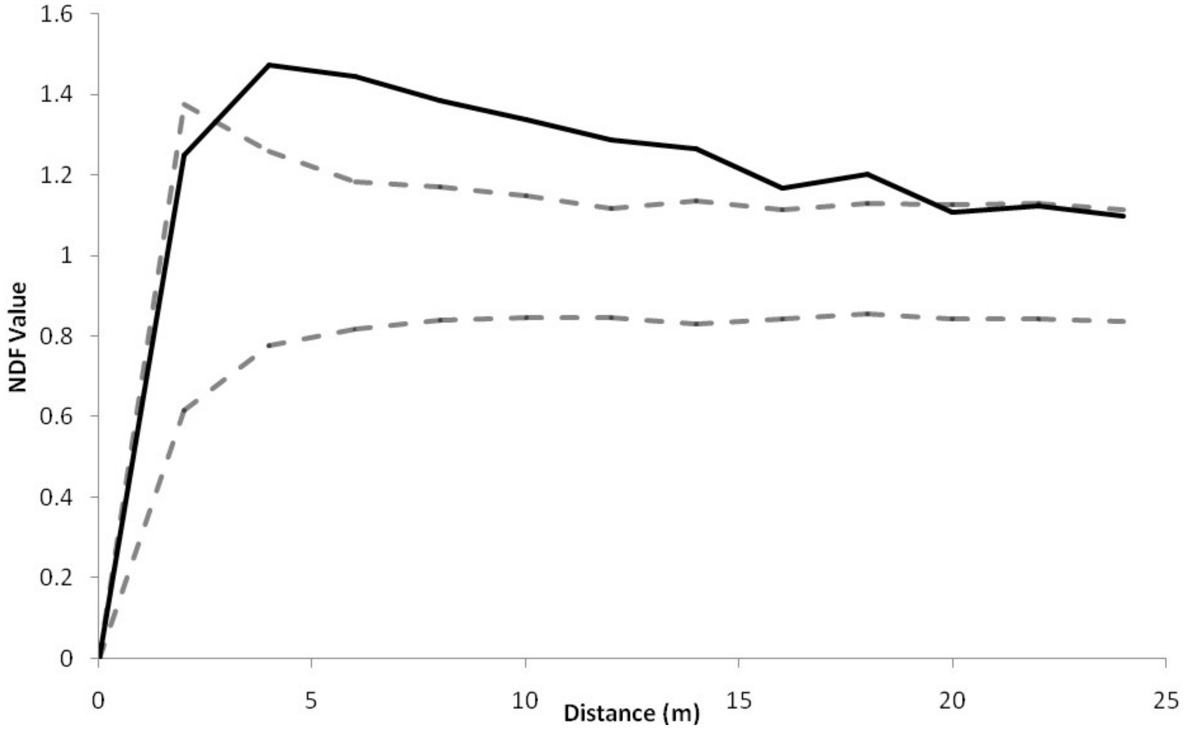

Figure 6. Bivariate NDF analysis of spruce and rocks. The dashed lines represent a 95% confidence interval, while the solid line represents the calculated NDF value.