Scale-dependent Interactions and Population Structure of *Abies lasiocarpa* Establishment along an Elevation Gradient of Subalpine Meadows

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Abstract

This study evaluates the importance of scale-dependent influences of dispersal and establishment on the population structure of conifers that are invading subalpine meadows. The spatial pattern of tree invasion was examined using a multi-distance spatial analysis to describe and understand these patterns. Meadows showed clumped spatial associations for seedling establishment, with larger trees and seedlings having strong spatial associations over a range of neighborhood sites indicating contagious dispersion. Observed differences in the spatial patterns of conifer invasion show instability in meadow to forest boundaries that is pronounced along the elevation gradient in both erosional and depositional meadows. Increased expansion of forests into meadows over time appears to occur in periods of favorable climate. The patterns of *A. lasiocarpa* invasion showed differences over distance across meadow-forest boundaries attributed to strategies in competition and facilitation and variations in soil and topography.

Key words: Scale-dependence; Competition; Facilitation; Tree invasion

1. Introduction

Mechanisms that structure vegetative populations and communities are a central topic in plant ecology (Watt, 1947). To understand the overall plant community pattern, it is essential to understand the mechanisms that shape the spatial pattern of individual organisms at fine scales. Studies have shown spatial pattern can represent facilitation and competition among populations because these patterns are linked to the overall processes that create them (Silvertown et al., 1992; Cairns et al., 2008; Kim et al., 2009). Patterns of scale dependent recruitment, or recruitment dependent upon meadow clearing size, are associated with successful establishment of adults and determine patch convergence or divergence from the community (Methratta and Petraitis, 2008).

Competition and facilitation are factors that influence population and community factors within the alpine and subalpine zones (Callaway and Walker, 1997; Callaway 1998; Choler et al., 2001; Callaway et al., 2002). Stress tolerance, facilitation, and competition are mechanisms used by plants to survive in marginal habitats (Grimes, 2001). In habitats where stress conditions prevail, seedling establishment advances under protective canopies of well established trees that reduce water and heat stress (Franco and Nobel, 1989; Callaway and Walker, 1997; Grime, 2001). Competition is thought to be important under conditions where resources limit productivity (Weins, 1977; Tilman, 1982). Tilman (1982) defined strong competitors as those individuals having the ability to tolerate extremely low resource levels. Such a definition focuses more on a mechanistic view of competition, but this view becomes more complex in light of plants modifying the environment to less favorable conditions making it unsuitable for the fitness of neighbors (Grime, 2001).

Subalpine meadows are maintained through a variety of factors, but are predominantly maintained via climate or through interactions of climate and fire (Agee and Smith, 1984; Butler, 1986; Taylor, 1990; Lepofsky et al., 2003). Changes in subalpine meadow size and distribution may be influenced by changes in temperature, snowpack, fire, grazing and other factors (Fonda and Canaday, 1974). Studies have shown an increase in the recruitment, growth, and distributions of subalpine conifer species in western North America (Innes, 1991; Little, 1994; Rochefort et al., 1994; Hessl and Baker, 1997). Studies show increased invasions and tree establishment in the Rocky Mountains during a warmer, wetter period in the 1940s and 1950s (Butler, 1986; Dunwiddie, 1977; Koterba and Habeck, 1971; Vale, 1981).

The tree invasion patterns observed in the subalpine forest-meadow ecotone show a pattern of restructuring at broad, regional scales. Few studies of seedling recruitment in subalpine meadow ecotones have been performed on the east side of the Continental Divide. This research seeks to fill this knowledge gap to better inform the mechanisms facilitating seedling invasion into meadows. The recent encroachment of trees is threatening to enclose Glacier National Park's subalpine meadows, which may alter meadow structure and composition important for foraging wildlife requirements (Lepofsky et al., 2003). The goals of this research are to analyze and characterize spatial patterns of conifer invasions into the subalpine meadows of Glacier National Park and to evaluate processes that may contribute to their invasions. Specifically, this study examined how competition by and facilitation of neighboring vegetation contribute to the pattern of conifer invasion.

2. Study Area

We conducted this research in Preston Park, Glacier National Park, Montana (48° 42' 5.22"N, 113° 40' 10.5234"W). Glacier National Park was established in 1910 and encompasses a total of 410,000 ha. The climate in western Montana is a highland complex contained in a continental, semiarid zone resulting in pronounced climatic variability over small spatial scales of a few kilometers (Bamberg and Major, 1968). The Continental Divide exerts a continental influence on the eastern side with the east side of the park, which is slightly drier relative to the western side (Rockwell, 1995). Climate stations near Preston, such as St. Mary and East Glacier receive in the range between 66 cm and 76 cm of precipitation respectively. Historically, rainfall accounts for a small fraction of the annual precipitation total as compared to snowfall. Subalpine forest and meadow soils for Glacier National Park are cold, moist soils Cryoboralfs and Cryoborolls, characterized as being saturated by winter snows (Anon, 1980; Butler and Malanson, 1989; Vogler, 1998). These are well drained soils with a depth to bedrock that is deep to very deep and are reflective of the parent materials (Vogler, 1998).

Tree species identified in the subalpine forests of Preston Park, Glacier National Park include *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), *Larix occidentalis* (Western larch), *Pinus contorta* (lodgepole pine) and *Pinus albicaulis* (whitebark pine). These species are located in subalpine zones at an elevation of 1,829 meters to 2,134 meters (Shaw and On, 1979). Field observations indicate that Preston Park's meadows are being invaded by conifer seedlings, with *A. lasiocarpa* seedlings being the most common seedling species observed.

3. Methods

3.1. Vegetative sampling and mapping

We targeted a single basin in Glacier National Park for sampling to limit the confounding influence of coarser scale geologic and climatic variability. Sites were sampled along an elevation gradient that took place in the summers of 2001 to 2003. Spatial characterization of conifer invasion into meadows was accomplished using a belt transect technique. Meadow boundaries were delineated as the break from mature forest with an herbaceous and grass species dominant area.

Based on visual estimation of obvious pattern, a measuring tape was used to demarcate a 10m swath containing the most apparent area of meadow invasion from forest boundary through the meadow to opposing forest boundary. The transect boundary was flagged and GPS locations were recorded at 2 m intervals along the belt-transect center line. A sketch of each 2 m by10 m section of the belt was drawn in the field, and the location of each individual tree was plotted by hand. Because meadow invasion was so dense at the higher elevations, a 5 m-wide belt transect was deemed sufficient to capture density and pattern. Methodical hand-drawn maps of the belt transects were used to determine the location of each individual with greater precision than a GPS which may log different trees at the same point.

3.2. Density mapping

The second-order neighborhood spatial analysis on Ripley's K function is used to analyze non-regular patterns of recruitment of woody species in harsh physical environments. This method requires a circle of radius t to be placed around each sample point, which in this study represents a tree, and the number of neighboring trees within the circle are counted. For our data, the radius of t is greater that mapped plots as the bounding polygon was larger to accommodate all sampling points. Points positioned close to the boundary of the sampling plot require a weighted edge correction (Haase, 1995; Haase et al., 1996):

$$K(t) = \sqrt{[K(t)/\pi]} - t$$

As the points are Poisson random and the cumulative function K(t) equals πt2, we plot the derived sample statistic $\sqrt{[K(t)/\pi]} - t$ as suggested by Skarpe (1991) and Haase et al. (1996).

For statistical significance, the lowest and highest values of the spatial statistic using 99 randomizations to define the lower and upper boundaries of the 95% confidence interval were used. If the sample statistic deviates outside the confidence interval, then there is a departure from random pattern. If the departure from the sample statistic is positive, then a clustered distribution is suggested. If the departure from the sample statistic is below the confidence interval, then a regular or uniform pattern is suggested. If the sample statistic remains within the boundary of the confidence interval, then a random pattern is suggested (Haase et al. 1996).

4. Results

The second order spatial analysis revealed significantly clumped spatial distribution of seedlings at a range of scales for meadows 1, 4, 6,7, 8, and ribbon forest 9 (Figure 1 a, d, f, g, h, i). Meadow 2, a dry meadow, showed a clumped pattern over 2 m, random pattern from 3 to 4m, and regular pattern from 4m and greater (Figure 1 b). Meadow 5 exhibits clustering spatial associations at scales less than 8.5 m distance, then a random pattern of spatial associations is present (Figure 1 e). Meadow 3, a small meadow, shows a random pattern within the 0-2 m and 5-6 m distance classes (Figure 1 c and g).

The second order spatial analysis revealed significant trends in spatial patterns for large (> 5 cm diameter) versus small trees (< 5 cm diameter). Meadow 1 show a strong spatial associations for large and small trees across the entire range of neighborhood sizes (Figure 2 a). Meadow 2 small trees show strong spatial associations for large and small trees across the entire range of the neighborhood (Figure 2 b). Meadow 3 shows a random pattern of trees across the neighborhood with the exception of 3 to 4.5m where strong spatial associations are shown (Figure 2 c). The small and large trees show a greater extent of clumping over the 3 to 4.5m distances (Figure 2 d). Meadow 4 large trees show a lesser extent of clumping over 6m distance and random pattern over greater distances (Figure 2 d). Meadows 5, 6, and 7 shows clumped spatial associations for small seedlings and larger trees the entire range of the neighborhood (Figure 2 e-g). Meadow 7 shows a random pattern for both small and large trees over total distances (Figure 2 g). Meadow 8 shows one of the strongest spatial associations compared to all the meadows across the entire range of the neighborhood (Figure 2 h). Meadow 9 shows a weak, positive spatial associations between seedlings and larger trees across the extent of the neighborhood (Figure 2 i).

Based on the bivariate second order neighborhood analysis all meadows, with the exception of meadow 3, show strong spatial associations between seedlings and trees across the entire range of the neighborhood for the transect (Figure 2 a-i). The patterns of establishment across the elevation gradient reflect larger, older trees recruiting seedlings in close proximity to the large individual (Figure 2 a-i). Near forest edges individuals tend to occupy available spaces (Figure 2 a-i). This recruitment is spreading into the slopes of the meadow boundaries and central meadow locations as tree islands (Figure 2 a-i). A t higher elevations and in ribbon forests, larger and smaller trees are more clustered together (Figure 2 a-i). In all meadows seedlings recruit with greater density around larger trees, but meadow 2 shows dispersion with greater distances from large individuals into more

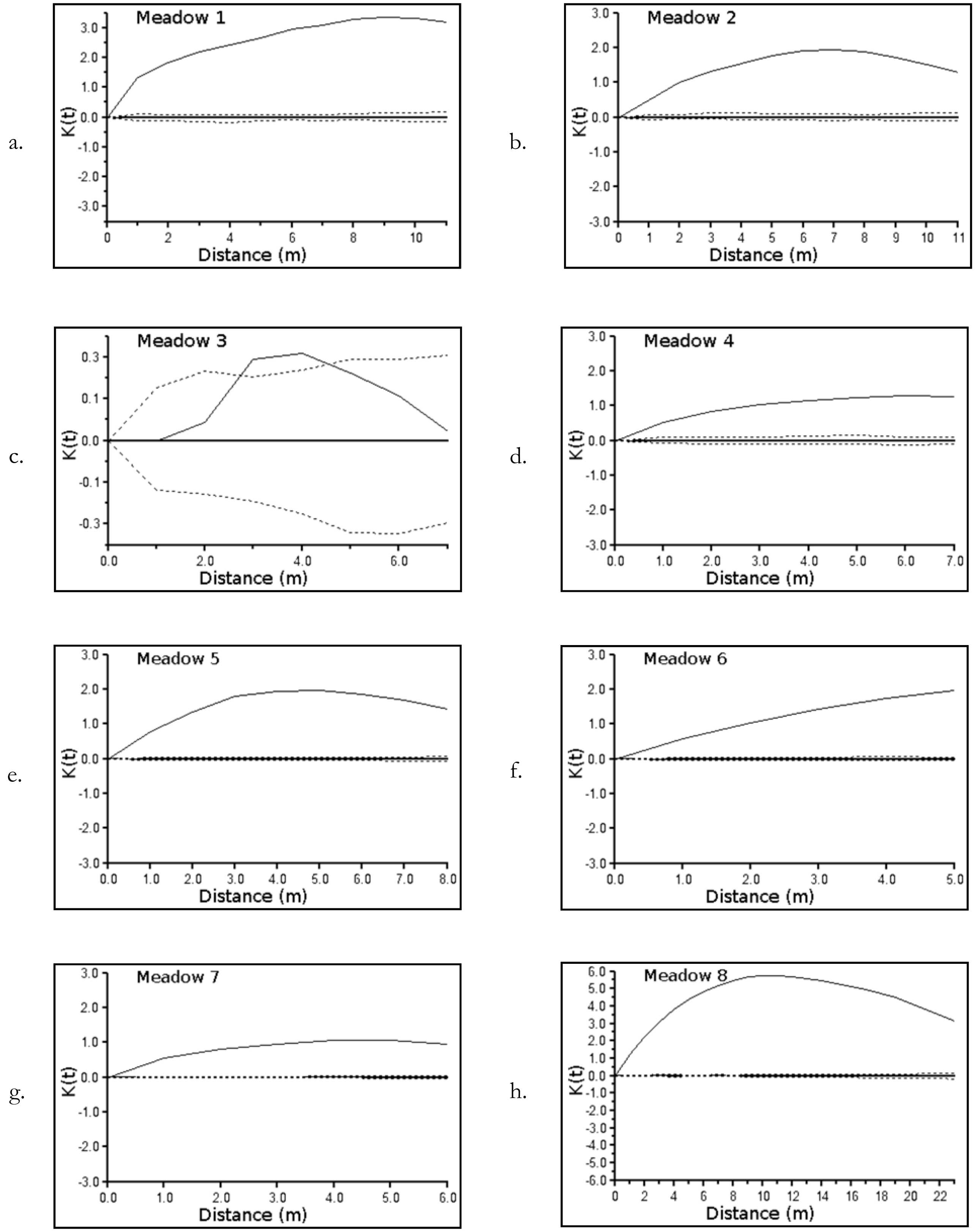


Figure 1. (a-i). Second-order neighborhood analysis results for *Abies lasiocarpa* in each meadow-forest boundary. Positive K(t) values indicates clustering while negative K(t) values indicate regular dispersion. Dashed line indicates the 95% confidence interval for departure of randomness constructed using Monte Carlo simulations. The x-axis denotes the distance (m) for the radius of the neighborhood for a given L(d) value.

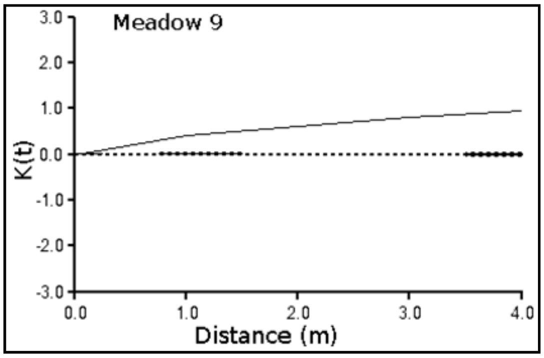
i. 

Figure 1. (i). Continued from above. See page 4 for description.

open sites (Figure 2 b). The meadow 2 pattern of closely clumped small trees around larger individuals shows avoidance of less favorable sites. Seedling recruitment in close proximity to larger trees in meadows across the elevation gradient, points strongly to the effects of positive feedback with intraspecific interactions (Figure 3 a-c).

5. Discussion

Pattern of *A. lasiocarpa* population establishment indicate mechanisms related to the regeneration niche and environmental gradients. The strongly clustered spatial patterns across spatial scales indicate that intraspecific interactions and life history are important controls of *A. lasiocarpa* establishment patterns. Stress tolerance and facilitation are two mechanisms used by *A. lasiocarpa* in establishment of subalpine meadows. Scale dependence is key to understanding the pattern of these intra-specific interactions.

The forest edge effect improves microsite and microclimate conditions and reduces limitations on *A. lasiocarpa* establishment (Liguna et al., 2008). Tree patches are known to ameliorate microsite conditions in the high mountain environments to facilitate invasion (Callaway, 1998). Canopies protect seedlings in the extreme conditions of high mountain environments. Larger individuals buffer the effects of a high irradiance environment, which can be deleterious to younger *A. lasiocarpa* seedlings (Germino and Smith, 1999). Exposure to solar radiation can also dry soils more rapidly early in the growing season creating drought stress for young seedlings with less established root systems. The snowpack melts earlier surrounding the larger individual, making surrounding sites open and available to seeds earlier in the growing season (Payette et al., 2001). Once established, seedlings are shade tolerant, flourishing in the shaded openings of the forest or in the shadows of trees on the edge of open sites in central meadow locations.

Seedling response to neighboring plants is important in structuring forests (Maher and Germino, 2006). Continued dominance of *A. lasiocarpa* within subalpine forests is predicted due to the presence of seedling establishment into meadows (Watt, 1947). The presence of a greater number of seedlings near larger trees shows the larger individuals increase seedling survival and increase seed deposits in the existing seed bank in close proximity (Tranquillini, 1979; Maher and Germino, 2006). Propagules are recruited heavily from the surrounding forests and from individuals well established in meadow interiors and produce seeds under more shaded canopies. Patterns of Preston Park *A. lasiocarpa* recruitment indicate that tree establishment for all sites show an "in-filling" process. An "in-filling" pattern is a result of seedlings establishing in more open gaps around larger individuals or patches of trees (Slatyer and Noble, 1992; Liguna et al., 2008). Larger trees establish on more favorable sites. These pioneer trees are key since they may be necessary precursors for in-filling" (Resler, 2006). Over time large individuals ameliorate site conditions creating sites conditions favorable to seedling establishment, or "in-growth" trees, i.e. "smaller diameter, shade tolerant species in high density clusters" (Smith et al., 2005). As climate favors reproduction for *A. lasiocarpa*, seeds of neighboring *A. lasiocarpa* individuals become deposited around larger trees on these favorable sites. In meadow 4, the pattern of large and small individuals located across the meadow boundary suggests that the presence of larger trees throughout both forest and meadow boundaries recruit small individuals heavily in all meadow locations (Figure 3 d). The increased tree island expansion seems to be infilling meadows and closing forest canopy more rapidly. For example, meadow 3 is small in size, and shows a greater amount of "in-filling" with greater canopy closure showing a more random pattern (Figure 3c). Meadow 3 is small compared to the rest of the meadows in the study, so canopy closure is more likely. Meadow 3 had many large individuals in the meadow interior.

At both the higher and lower elevation sites seedlings and saplings of *A. lasiocarpa* establish in close spatial proximity to large trees. The dense clusters for all meadows, with exception of meadow 3, show that at the seedling stage the facilitative effects of larger individuals are important for seedling survival. In the more open meadows of Preston Park, especially in

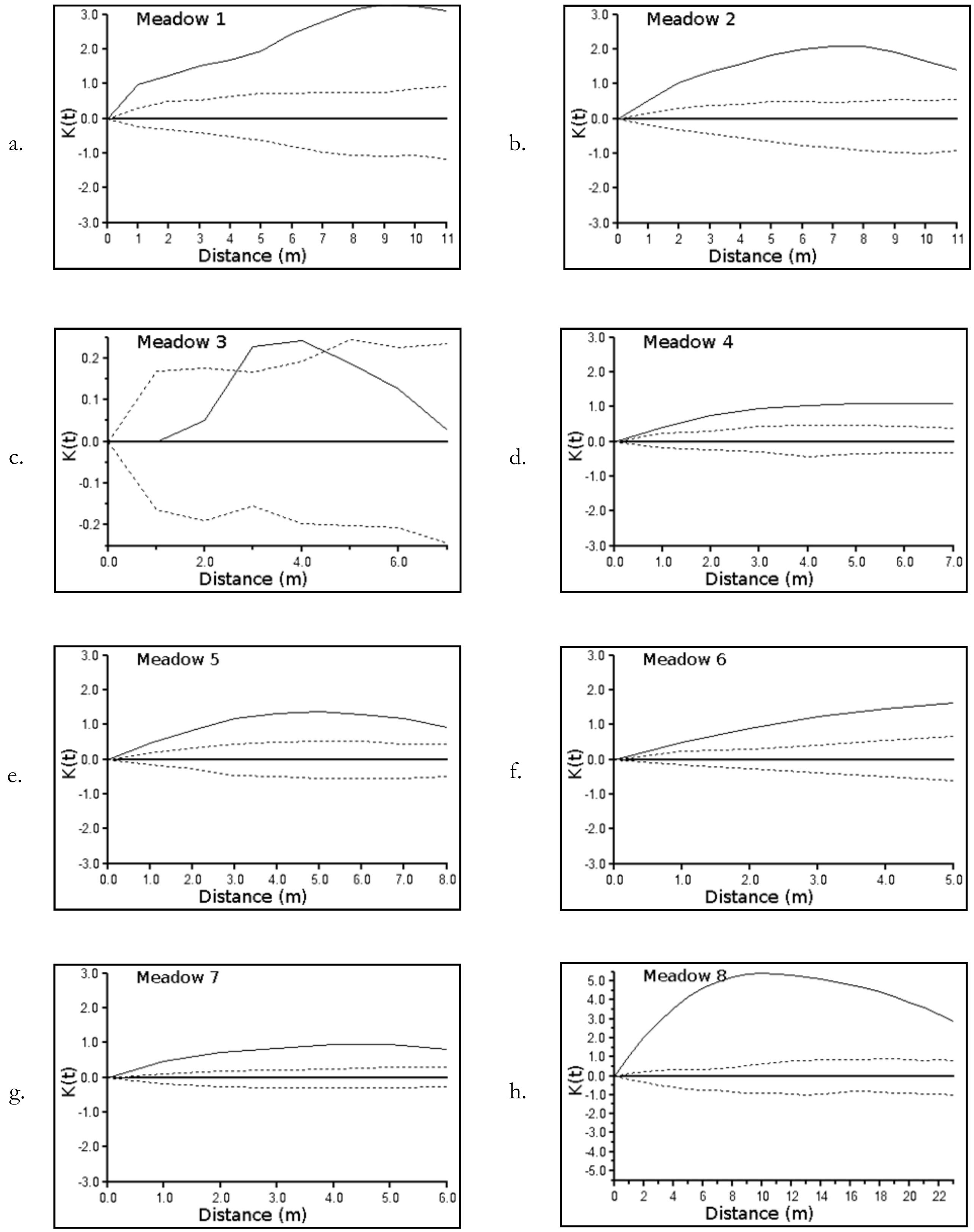


Figure 2. (a-i). Bivariate second-order neighborhood analysis results for Abies lasiocarpa in each meadow-forest boundary subdivided by <5cm diameter class or > 5 cm diameter class. Positive K(t) values indicates clustering while negative L(d) values indicate regular dispersion. Dashed line indicates the 95% confidence interval for departure of randomness constructed using Monte Carlo simulations. The x-axis denotes the distance (m) for the radius of the neighborhood for a given K(t) value.

i.

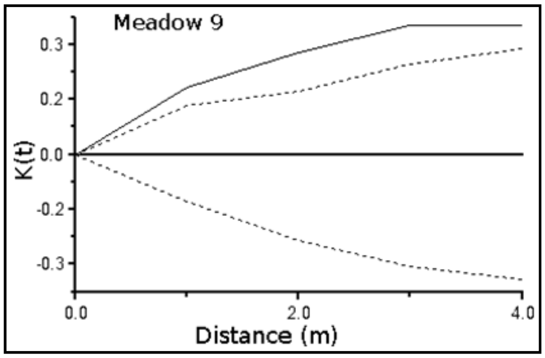


Figure 2. (i). Continued from above. See page 6 for description.

a.
b.
c.

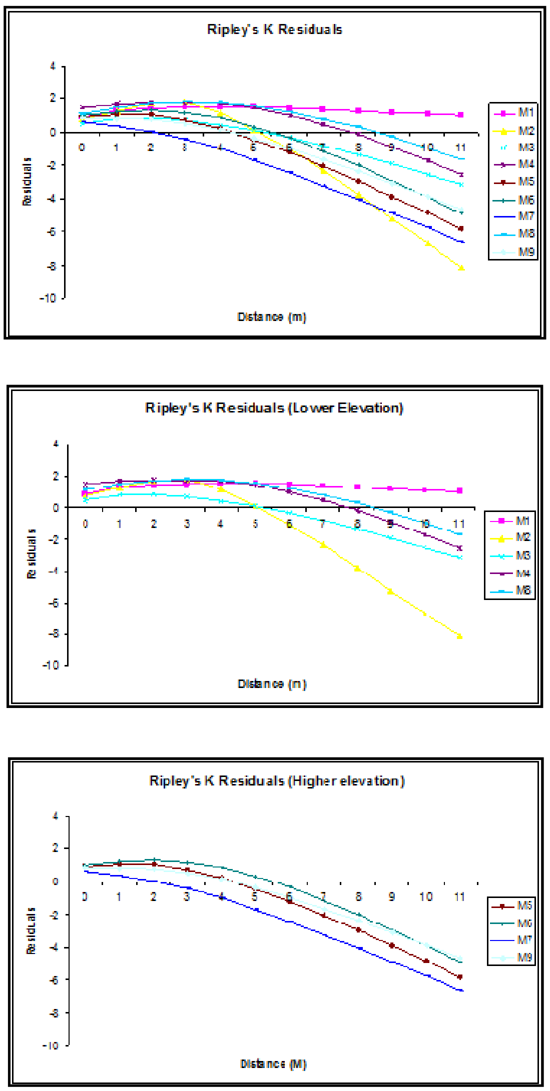


Figure 3. (a-c). Ripley's K residual grouped a) all meadows, b) lower elevation meadows, c) higher elevation meadows

meadow interiors, these individuals are more sparse and are shorter statured. Resource constraints express a similar pattern for all meadows on the elevation and topographic gradient with the exception of meadows 5, 8, and 9; and the lack of individuals at lower meadow and forest boundaries may reflect sites with inadequate resources for germination and establishment of seedlings. Compared to the other meadows in this study, meadows 5, 8, 9 are more eroded, more deeply incised stream channels, and have steeper slopes than lower meadows. These characteristics are likely to produce a more pronounced "snow fence" effect where wind blown snow accumulates, and persists on the landscape for a longer time and shortens the growing season in these specific locations. Limiting factors, such as soil moisture and intense solar radiation, are strong controls on this establishment pattern. In tree islands and meadow "rims" organic matter is more plentiful and soil depth is greater. Butler et al. (2003) found in Preston Park that meadow and ribbon forest "rims", locations where A. lasiocarpa establishment is most clumped, had greater organic matter and alluvium present and central meadow interiors had less organic matter and colluvium present. Our findings suggest topographic influence may be a factor on seedling establishment pattern. For example a majority of the establishment occurs on the hotter, drier aspects positioned on the south, southwest, and west facing slopes.

Scale-dependency is key to understanding how competition and facilitation influence population spatial structure. Scarcity of resources may amplify the competitive effect when considering intra-specific competition across the landscape. Environmental conditions may reduce the competitive ability of smaller individuals within the same species. Though *A. lasiocarpa* is a hardy and long lived competitor, smaller individuals face competition from herbaceous species as primary competitors for water and nutrients in more central meadow locations. Even with a favorable growing season that contributes to growth, maintenance and reproduction; smaller *A. lasiocarpa* individuals can be outcompeted by larger neighbors. So under strained resources and on unfavorable sites, as found in more central meadow locations, larger trees will facilitate their neighbors. Since *A. lasiocarpa* is a long-lived and hardy competitor, it dominates high elevation forests and influences successional dynamics over a longer period of time (Watt, 1947; Liguna et al., 2008).

6. Summary and Conclusions

Population patterns in subalpine meadows and ribbon forests of Preston Park seem to reflect positive feedback effects (cf. Wilson and Agnew, 1992). The buffering of negative climate conditions is crucial for seedlings to survive during periods when climate is not optimal for further seedling advancement. Because data collection of smaller trees was restricted by the National Park Service, it is difficult to discern if climate has had an effect on contemporary establishment patterns. There is a strong spatial association of large trees and seedlings in the subalpine meadows in Preston Park, GNP. The continued facilitation of seedlings by trees may "in-fill" and meadows will become more closed canopied in response to continuing climate change that is favorable for establishment.

Topography influences the spatial patterns of soil nutrients moisture and temperature, as well as influences the amount and duration of snowpack within Preston Park meadows and ribbon forests. Establishment, especially tree patches or tree islands, seems to track deeper soil resources, or deeper soils form because of the tree islands. These factors in turn influence the spatial patterns of *A. lasiocarpa* in Preston Park meadows and forests. Climate has more indirect effects on environmental heterogeneity and the role of competitive hierarchical interaction between individuals of *A. lasiocarpa*. Because *A. lasiocarpa* establishes on severe sites under these climate conditions it may continue to dominate subalpine forests unless disturbance enters the basin. In the presence of a hotter, drier climate paired with a reduced snowpack that extends the growing season, *A. lasiocarpa* recruitment in forests may increase, but this climate could maintain meadows with more shallow, drier soils. Periods of cooler, wetter climate may continue to destabilize the meadow to forest boundaries and recruit seedlings into meadow interiors where soil resources are available.

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