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Modeled Seed Accumulation Patterns Explain Spatial Heterogeneity of Shrub Recruitment Within the Taiga-Tundra Ecotone

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Key Points:

- We examined the mechanisms controlling fine-scale patterns of tall shrub recruitment at a taiga-tundra ecotone site
- Seedling abundance was well explained by models of seed dispersal, suggesting seed limitation likely constrains recruitment
- Topographic controls on recruitment were weaker than elsewhere in the Arctic, however, ground cover remained a key environmental filter

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Arctic shrub productivity trends display variability at multiple spatial scales. Fine-scale studies have generally observed the greatest shrub expansion in landscape positions that accumulate water and nutrients. While considerable work has focused on the mediating effect of these resources on growth responses to warming, less is known about the mechanisms constraining recruitment-driven expansion. Given the low seed viability of many Arctic shrubs, spatial patterns of seed dispersal may play an important role in constraining fine-scale variability of shrub recruitment. This variability may also be driven by ground cover suitability, though these relationships are understudied in undisturbed sites. Here, we developed models representing seed accumulation mechanisms around *Alnus alnobetula* (green alder) patches within the taiga-tundra ecotone of the Northwest Territories and compared these with observations of seed and seedling density. We also investigated relationships between seedling abundance, topographic position, and ground cover. Observed patterns of recruitment were complex, with preferential expansion occurring beneath alder patches only on the steepest slopes. Seed accumulation models representing overland flow, wind, and source distance were important predictors of seedling recruitment. This provides indirect evidence of localized seed limitation around patches, suggesting future recruitment may not respond as expected to changing environmental conditions. *Sphagnum* cover also predicted recruitment, indicating the importance of seedbed conditions for establishment. We propose that developing models of shrub expansion that include both dispersal and environmental constraints may increase our ability to predict patterns and rates of expansion. Such predictions are necessary to understand future biosphere-atmosphere interactions in a rapidly changing Arctic.

Plain Language Summary Shrubs are becoming larger and more common across the Arctic, but the magnitude of this change is not the same everywhere. The strongest increases in shrubs are generally observed in valley bottoms and drainage channels, a trend often attributed to greater moisture and nutrient availability. Alternatively, these non-uniform increases in shrub cover may be caused by low quality seed being spread unevenly across the landscape, such that new shrubs primarily occur at locations receiving the most seed. Ground covers like mosses and lichens may also control where new shrubs survive. Here, we compared observed numbers of seeds and seedlings to modeled predictions of seed input around green alder patches in the taiga-tundra transition zone. We also compared the number of seedlings among different hillslope positions and ground cover types. Seedlings were most commonly found where our models predicted seed would arrive if carried by both water and wind, although this was constrained by distance from patch. They also occurred most often in places where *Sphagnum* mosses were abundant. The importance of seed arrival and the limited importance of hillslope position suggest that both seed availability and environmental suitability may be important for predicting the location of future shrubs.

1. Introduction

The density, cover, and growth rates of deciduous shrubs are increasing across much of the Arctic though this trend displays variability at fine and coarse scales (Frost et al., 2013; Myers-Smith et al., 2011, 2020; Ropars & Boudreau, 2012; Ropars et al., 2015). Many fine-scale studies have documented preferential increases in shrub cover and recruitment at the base of slopes, in valley bottoms, and in other areas that accumulate water (Cameron & Lantz, 2016; Naito & Cairns, 2011; Tape et al., 2006). This relationship between shrub expansion and

landscape position is generally attributed to a spatially constrained release of moisture and/or nutrient limitation, which enhances the response of shrubs to climate warming (Campbell et al., 2021; Tape et al., 2012). While the mediating effect of moisture and nutrient availability on individual shrub productivity responses to warming has been well studied (Chapin et al., 1995; Elmendorf et al., 2012; Myers-Smith et al., 2015), less is known about the specific mechanisms behind recruitment-related expansion. This is an increasingly important knowledge gap as shrub species have increased both reproductive effort and success in response to warming (Klady et al., 2011) and there is evidence that colonization by sexual reproduction has contributed to the recent expansion of multiple tall shrub species (Lantz et al., 2013; Tremblay et al., 2012). Tundra shrubs have been shown to influence a wide range of ecosystem properties such as snow accumulation (Pomeroy et al., 1993; Sturm et al., 2001), surface energy balance (Chapin et al., 2005; Marsh et al., 2010; Sturm, 2005), wildlife habitat availability (Boelman et al., 2014; Joly et al., 2010), permafrost conditions (Blok et al., 2010; Frost et al., 2018; Wilcox et al., 2019), and carbon cycling (Lafleur & Humphreys, 2018). As such, understanding the mechanisms driving fine-scale spatial variability in recruitment-driven shrub expansion is critical for predicting future changes in tundra ecosystem function as well as interactions between the biosphere and the atmosphere.

Fine-scale spatial variation in shrub recruitment is constrained by two primary factors: arrival of seed at a site and environmental conditions suitable for establishment and survival (Moore & Elmendorf, 2006). Microsites where increased seed addition results in greater recruitment are considered seed limited as population growth is constrained by seed abundance rather than environmental suitability (Aicher et al., 2011; Turnbull et al., 2000). This definition has also been extended to the landscape context such that sites with positive relationships between observed seed and recruitment density are generally considered seed limited (Aicher et al., 2011; Nathan & Muller-Landau, 2000; Norden et al., 2009). While hypotheses regarding preferential shrub recruitment have primarily focused on variation in environmental constraints (i.e., topographically derived resource gradients), it is also possible that seed limitation may play an important role in governing the spatial patterns of shrub recruitment. For example, the primary dispersal mechanism of a shrub species may exhibit spatial heterogeneity causing the probability of seed arrival to vary considerably across the landscape. Under these conditions the distribution of recruitment and establishment may be more a reflection of seed limitation than environmental conditions (Nathan & Muller-Landau, 2000). Heterogeneity in dispersal patterns may be particularly relevant to recruitment at the northern edge of species' ranges, where seed viability tends to be low (e.g., Lantz et al., 2010; Weis & Hermanutz, 1988). In these systems we might expect sites with the greatest seed input to support the most recruits and that meaningful establishment will occur only at sites that both accumulate sufficient numbers of seed and have appropriate environmental conditions. This scenario presents an alternative explanation for heterogeneous shrub expansion in which expansion patterns may be partially constrained by seed availability and the mechanisms that control seed accumulation.

Various physical mechanisms may contribute to non-uniform seed accumulation in tundra environments. For example, the process of overland, water-based dispersal, referred to herein as overland hydrochory, may result in seed accumulating in sites that are hydrologically connected to seed sources (Thompson et al., 2014). Reliance on hydrochory as a means of dispersal along river systems has been well documented for several of the shrub taxa undergoing expansion in the tundra (Merritt & Wohl, 2006; Rasran et al., 2021; Walker et al., 1986). While the specific importance of overland hydrochory in governing tundra shrub dispersal is less well known, there is evidence that surface runoff generated by melting snow drifts can contribute to the spatial pattern of seed dispersal in both alpine and Arctic tundra systems (Peringer & Rosenthal, 2011; Kołos & Banaszuk, 2018; C. Wallace, Personal observation). Seed deposition downwind of a seed source in regions with consistent prevailing winds (Kambo & Danby, 2018) and redistribution into snow drifts during blowing snow events (Larsson & Molau, 2001) are also potential seed accumulation mechanisms. Several of these mechanisms might promote seed accumulation in low-lying areas, leading to localized increases in recruitment and potentially confounding the distinction between environmental and seed dispersal-related drivers of recruitment. For these reasons, non-uniform seed accumulation may be an understudied cause of variability in fine-scale patterns of tundra shrub expansion.

Fine-scale spatial patterns of seedling recruitment may also relate to variation in microsite conditions and specifically, seedbed quality. Bare ground and moss substrates are important for successful *Salix* spp. germination (Angers-Blondin et al., 2018) and increased shrub growth and recruitment have been documented after disturbance events that expose mineral soil (e.g., Frost et al., 2013; Lantz, 2017; Lantz et al., 2013; Tremblay

et al., 2012). However, in situ relationships between ground cover and shrub seedling establishment in undisturbed environments have not been examined.

Improving our understanding of the mechanisms underlying fine-scale variability in shrub recruitment will support spatially explicit predictions of shrub expansion and future tundra ecosystem function. To this end, we ask: 1) Are patterns of tall shrub seedling recruitment topographically driven? 2a) Do hypothesized mechanisms (i.e., overland hydrochory, snow drifting, wind dispersal, and distance to seed source) of non-uniform seed accumulation explain the spatial distribution of seedling recruitment around shrub patches, 2b) How do models of these mechanisms perform relative to topographically derived environmental gradients? 3) Can the fine-scale relationships between mechanisms of seed accumulation and seedling density be extrapolated to a sub-basin scale? 4) Does the microsite ground cover influence establishment success once a seed has arrived?

2. Methods

2.1. Study Site

This study was performed in the Inuvialuit Settlement Region within a 2 km radius of the Trail Valley Creek Research Station (TVC) (Figure 1). TVC lies within the Trail Valley Creek watershed, located in the northern transition zone of the taiga-tundra ecotone approximately 50 km north of Inuvik, Northwest Territories, Canada (68°44'30.95"N, 133°29'56.54"W) (Lantz et al., 2010). The mean annual temperature in Inuvik is −7°C and average annual precipitation is 249.8 mm (1991–2020; ECCC, 2024). The terrain at TVC is underlain by continuous permafrost and consists of gentle hills and incised river valleys. Soils generally contain an organic horizon comprised of either humified peat or living mosses (e.g., *Sphagnum* spp., *Hylocomium splendens* (Hedw.) Schimp., *Dicranum* spp.) overlying fine-grained mineral soils that developed from ice-rich morainal deposits (Aylsworth et al., 2000). The vegetation is primarily characterized by communities of tall deciduous shrubs such as *Alnus alnobetula* (Ehrhart) K. Koch (green alder), surrounded by open tundra (referred to herein as alder-free tundra) dominated by dwarf shrubs (e.g., *Rhododendron tomentosum* Harmaja, *Vaccinium vitis-idaea* L.), sedges (*Eriophorum* spp., *Carex* spp.), and reindeer lichens (*Cladonia* spp.).

To address our research questions, we focused on the fine-scale variability of green alder dispersal and recruitment. The growth of green alder has been shown to be particularly sensitive to climate across much of the Arctic (Myers-Smith et al., 2015), and the density of the species has increased rapidly in our study region over the latter part of the 20th century (Lantz et al., 2013). As a nitrogen-fixing shrub, the expansion of green alder has enhanced potential to alter biogeochemical cycling at the taiga-tundra ecotone (Densmore, 2005). In this region alder generally grows in discrete patches across the landscape. These patches capture snow very effectively due to the height of alder relative to surrounding vegetation and are therefore hydrologically important in the region (Marsh et al., 2010; Wilcox et al., 2019). We focus on alder here in part due to this capacity for modifying its local environment (Wallace & Baltzer, 2020) as well as it being the subject of previous studies of shrub expansion heterogeneity in Northwestern North America (e.g., Tape et al., 2012).

2.2. General Statistical Approach

In this study we used an information-theoretic approach to quantify the relative strength of competing alternative hypotheses (i.e., a priori candidate models) (*sensu* Anderson, 2008). Each of our four primary questions was addressed by comparing a different set of ecologically relevant models. All model sets also included an intercept-only model which included no predictor variables. Inclusion of an intercept-only model is recommended when it is plausible that none of the hypothesized models improves on using the mean of the response variable to predict all sample values, essentially serving as a null model (Anderson, 2008). For each model in a set, we used model.sel() from the 'MuMIn' package (version 1.43.45; Bartoń, 2019) to calculate the corrected Akaike Information Criteria (AICc), the log likelihood, and the model weight to assess the probability that an individual model was the most likely in the set given the available data (Anderson, 2008). To avoid issues of multicollinearity we removed variables with a variance inflation factor (VIF) greater than 3 or with a correlation coefficient greater than 0.5 (Harrison et al., 2018). All statistical analyses were performed in the *R* statistical environment version 3.6.2 (R Core Team, 2019).

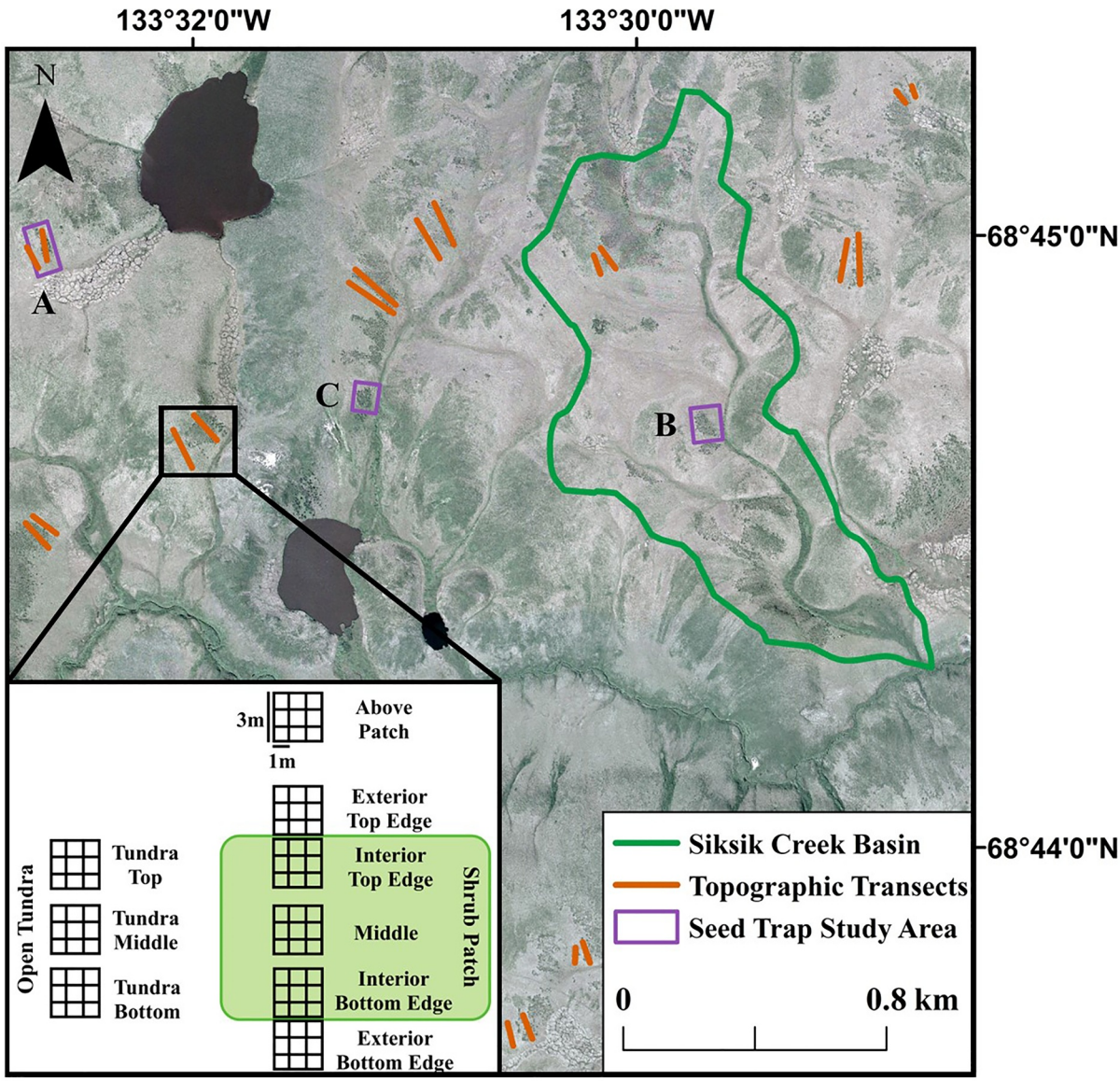

Figure 1. Location of topographic position transects, seed trap grids at the Trail Valley Creek Research Station, and modeled sub-basin (Siksik Creek). The polygons associated the seed trap study area represent the outer perimeter of the seed trap grid. Orthoimagery was collected during the summer of 2004 (GNWT Center for Geomatics, Mackenzie Valley OrthoPhoto Cached Mosaic Service https://www.geomatics.gov.nt.ca/en) **Inset:** Sampling layout for determining topographic patterns of seedling abundance (Question 1) and ground cover establishment (Question 4). "Open tundra" refers to alder-free tundra adjacent to an alder patch.

2.3. Topographic Patterns of Recruitment (Question 1)

To determine whether patterns of alder seedling recruitment were associated with topographic position, we performed seedling counts along two transects at 10 sites (Figure 1). At each site, one transect ran from the top of the hillslope to the bottom through an alder shrub patch and the other ran parallel to the first but in the adjacent alder-free tundra. The patch transect contained six 9 m^2 quadrats at the following slope positions: (a) 10 m above the patch ("Above Patch"); (b) the top exterior edge of the patch ("Exterior Top Edge"); (c) the top interior edge ("Interior Top Edge"); (d) the patch middle ("Middle"); (e) the bottom interior of the patch ("Interior Bottom Edge"); and (f) the bottom exterior of the patch ("Exterior Bottom Edge"). The tundra transect had three 9 m^2 quadrats at the same slope positions as 3, 4, and 5, labeled "Tundra Top", "Tundra Middle", "Tundra Bottom" respectively. Each of these quadrats was sub-divided into nine 1 m^2 sub-plots. Two of these sub-plots were randomly selected and the number of alder seedlings occurring within each sub-plot was recorded (Figure 1 Inset). The seedling data collected along the patch transects were then analyzed by comparing a model that included

Table 1
Hypothesized Mechanisms of Seed Dispersal

Accumulation mechanism	Ecological explanation	Mechanistic model representation	References
Overland Hydrochory	• Overland hydrochory is the process of seed transport via overland flow[1]. • Seed transport by overland flow is an important mode of dispersal in arid ecosystems[2]. • Seed may be carried downslope in meltwater streams while the frost table is near the ground surface. • The most seed would be expected at points which were most hydrologically connected to seed sources.	The value of Overland Hydrochory (OVERLAND) for a given point represents the number of shrub patch pixels within the contributing area of that point defined by the flow accumulation of a 5 m DEM.	1. Thompson et al. (2014) 2. García-Fayos et al. (2010)
Wind Dispersal	• Wind dispersal is the process of windblown seed transport. • It may lead to accumulation in regions with strong prevailing wind directions, such that most seed would be expected downwind of seed sources[3]. • In this study we focus on the dominant winter wind direction due to the timing of seed release[4].	The value of Wind Dispersal (WIND) for a given point represents the number of shrub patch pixels within the contributing area of that point defined by all pixels which lie in the region between 112.5 and 157.5 degrees of the point.	3. Kambo & Danby, (2018) 4. Jones & del Moral, (2005)
Snow Dispersal	• As snow is redistributed across the landscape, seed may be carried with it and deposited in the same locations snow accumulates[5]. • Snow drifts would be expected to have more seed than non-drift locations.	The value of the Snow Dispersal "model" (SNOW) represents the presence/absence of a given point in a snow drift, defined as LiDAR derived snow depth greater than 1 m. Seed density is assumed to increase in drifts.	5. Larsson & Molau (2001)
Distance from Source	• Seed may be most numerous at locations nearest seed sources, regardless of the direction to the source[6].	The value of the Distance from Source (DISTANCE) variable represents the distance from the nearest alder patch. Seed density is assumed to decrease linearly with distance.	6. Nathan & Muller-Landau (2000)

Note. Columns represent the ecological rationale behind the mechanism and the implementation of the model representing the mechanism.

topographic position as a fixed effect to a null model (Anderson, 2008; Burnham et al., 2011). This was done using linear mixed effects models with seedling count as the response variable and site as a random effect (lmer(); lme4; version 1.1–21; Bates et al., 2015). Seedling counts were log-transformed to meet the assumptions of mixed effects models. Since only one of 30 quadrats in the tundra habitat contained seedlings, the tundra habitat transects were not included in this analysis. Because seedling establishment was highly variable across patches, we also tested if preferential recruitment at slope bottoms was explained by the steepness of the hillslope at each patch. To do this we subtracted the number of seedlings observed in the Exterior Top Edge quadrats, from the number of seedlings observed in the Exterior Bottom Edge quadrats of each patch (Figure 1 Inset) and modeled this variable as a function of hillslope steepness using linear regression.

2.4. Fine-Scale Mechanisms Controlling Seedling Distributions (Question 2)

2.4.1. Field Sampling and Mechanistic Model Development

To investigate mechanisms controlling the fine-scale distributions of seedlings around alder patches we selected three alder patch sites and established a grid of sampling locations at intervals of approximately 15 m such that the

grid entirely encompassed each patch (Figure 1). Capturing the entirety of each target patch was essential to ensure an accurate, spatially explicit representation of recruitment patterns. Patch selection therefore required targeting patches with smaller than average areal extents, as fully encompassing larger patches was not logistically feasible. Sample patches were representative of larger alder patches at the site with respect to stem density, height, and positioning on the hillslope. Seed traps made of plastic garden trays and artificial turf were deployed in August 2016, and collected in June 2017 to capture peak alder seed rain (Bonner, 2008) and seed that was subsequently redistributed via blowing snow. We also counted seedlings in a 2 m^2 quadrat placed immediately to the right of each seed trap location. These data were then compared to mechanistic models consistent with four modes of seed dispersal: (a) overland hydrochory (hereafter referred to as OVERLAND when referring to the model), (b) wind dispersal (WIND), (c) snow dispersal (SNOW), and (d) a model treating seed density as a function of distance from seed source (DISTANCE) (Table 1). These models represent the capacity for seed arrival at each seed trap location (referred to as the "target point") for a given dispersal mechanism. All models were developed using ArcGIS (version 10.5, ESRI, Redlands, CA).

The OVERLAND and WIND models operate similarly by calculating a "contributing area" for each target point. In the OVERLAND model, the contributing area constitutes the area water would be expected to flow through before reaching the target point. To calculate this, we used a 1 m LiDAR Digital Elevation Model (DEM) created during snow-free conditions in August 2008 (Vertical accuracy: sd = 0.05 m; Hopkinson et al., 2011). This 1 m DEM was resampled into a 5 m DEM using bilinear interpolation to mitigate the influence of erroneous elevation data occasionally found in areas of tall/dense shrub patches. The resampled 5 m DEM was then used as input to the "Watershed" tool in ArcGIS which was run individually for each target point (Supplementary Figure S1 in Supporting Information S1). The contributing area for the WIND model constitutes the region northwest (between 112.5 and 157.5°) of the target point, which aligns with the dominant direction for winter wind speeds greater than 4 m/s at TVC as measured by the local meteorological station (Figure S2 in Supporting Information S1). To estimate the extent of the alder cover acting as a seed source inside the contributing area of each target point, alder patches were digitized using drone imagery of the site (~3 cm resolution) and the total number of alder pixels in the contributing area was summed. These sums act as a proxy for the relative quantity of seed expected at each point given the dispersal mechanism in question. In other words, these models assume that the greater area of alder patch represented in a contributing area, the greater potential for seed transport to the target point.

Snow depth at our study site is highly heterogenous due to the redistribution of snow from wind-exposed tundra to topographically derived drift locations and shrub patches during blowing snow events (Marsh & Pomeroy, 1996). The SNOW model is based on the assumption that alder seed is transported during these blowing snow events and that deeper drifts will hold more seed. This expectation is derived from the observations that green alder disperse their seed on top of the snow in late fall/early winter and that seeds are light enough to be transported by wind over the snow surface (Jones & del Moral, 2005). The SNOW model used a 2013 LiDAR snow depth product, which was based on the difference between the 2008 snow-free DEM mentioned previously and an April 2013 top-of-the-snow LiDAR DEM, to model the expectation that seed density would be greater in deeper snow (Table 1) (King et al., 2018). Despite the LiDAR snow depth product and the data for the current study being collected in different years, comparison to drone-derived snow depth data suggests a high degree of interannual stability in snow drift location (Supplementary Text S1 in Supporting Information S1). After conversion to a binary variable to minimize errors induced by tall vegetation canopies, the result was a raster of estimated drift locations for winter 2013 (Supplementary Text S1 in Supporting Information S1) used to estimate seed accumulation (Table 1).

The DISTANCE model addresses the hypothesis that seed density would decrease with distance from the seed source, regardless of the direction. It does this by simply assuming a negative linear relationship between the distance to an alder patch and the expected amount of seed at a given target point (Table 1).

In addition to the seed accumulation mechanisms described above (Table 1), we also calculated Topographic Wetness Index (TWI) as a proxy for topographically derived resource availability. TWI was calculated for each target point using the 5 m DEM as input for the Compound Topographic Index tool of the Geomorphometry and Gradient Metrics Toolbox (version 2.0–0; Evans et al., 2014). This variable was then included in the models of seedling recruitment to compare the explanatory power of seed accumulation mechanisms and environmental conditions on fine-scale seedling distributions (Question 2b).

Table 2
Model Set Used in AICc Model Selection to Address the Mechanisms Controlling Fine-Scale Variability in Seedling Abundance (Question 2a and b)

Seedling models								
							Pseudo R^2	
Model name	Model parameters	Log(L)	Δ AICc	w_i	Residual/null dev.	Residual/null df	Marg.	Cond.
Seedling1	TWI + OVERLAND + SNOW + **DISTANCE** + WIND	−165.485	0.00	0.999	331.0	163	0.226	0.226*
Seedling6	OVERLAND + **DISTANCE**	−175.285	13.15	0.001	350.6	166	0.187	0.202
Seedling10	OVERLAND + SNOW	−181.376	25.33	0	362.8	166	0.116	0.137
Seedling7	**DISTANCE** + WIND	−186.513	35.61	0	373.0	166	0.187	0.195
Seedling12	TWI + **DISTANCE**	−186.521	35.62	0	373.0	166	0.190	0.209
Seedling8	SNOW + **DISTANCE**	−189.129	40.84	0	378.3	166	0.166	0.186
Seedling5	**DISTANCE**	−192.518	45.52	0	385.0	167	0.171	0.193
Seedling9	SNOW + WIND	−193.564	49.71	0	387.1	166	0.093	0.104
Seedling2	OVERLAND	−196.713	53.91	0	393.4	167	0.028	0.069
Seedling15	**TWI** + OVERLAND	−196.699	55.98	0	393.4	166	0.029	0.068
Seedling4	SNOW	−200.796	62.08	0	401.6	167	0.077	0.105
Seedling13	TWI + SNOW	−200.509	63.60	0	401.0	166	0.077	0.105
Seedling3	WIND	−205.096	70.68	0	410.2	167	0.027	0.048
Seedling14	TWI + WIND	−204.371	71.32	0	408.7	166	0.029	0.052
Seedling11	TWI	−214.611	89.71	0	429.2	167	0.006	0.046
Seedling16	Null	−215.936	90.28	0	431.9	168	0	0.038

Note. Model parameters in bold were estimated to have negative coefficients during model fit. "Δ AICc" is the change in the corrected Akaike Information Criteria (AICc) between the target model and the next most likely model. "w_i" represents the model weight which gives the probability that the target model is the most likely model of the set. Deviance columns represent residual deviance for all models except the null model for which the null deviance is reported. Pseudo-R^2 is the trigamma Pseudo R^2-GLMM. An (*) indicates the conditional R^2 is equivalent to the marginal R^2 because no variance in the random effect was estimated. Each model in this model set was included in the model averaging of coefficients and predictions.

2.4.2. Statistical Models of Seedling Distributions

We created a set of statistical models representing our a priori expectations as to the most likely combinations of mechanisms controlling seedling distributions at our study site (Table 2, Tables S2, and S3 in Supporting Information S1). Models were included in model sets which represented individual hypothesized mechanisms in single variable models as well as models with select interactions among mechanisms (e.g., all mechanisms were included in models which allowed them to interact with DISTANCE). TWI was included as a single variable model as well as several models which allowed for an interaction with select dispersal mechanisms. A full model was included in which there is no single dominant dispersal mechanism hypothesized but rather that downslope resource gradients (TWI) and all dispersal mechanisms are expected to be moderately important (Table 1).

The above analyses were similarly run for the observed seed density data collected from the seed traps (Table S1 and Figure S3 in Supporting Information S1). However, in the spring following placement of the seed traps we observed seed being transported across the ground surface by meltwater (overland hydrochory) at several locations throughout TVC. As such, we suspect that our seed traps, which were placed on the ground surface, both missed seed that was redistributed by the flow of water and prevented captured seed from being transported by overland flow making these traps ill-suited for testing this mechanism of dispersal. If this is the case, analyses which compare seed trap data to the OVERLAND model are likely unreliable. Therefore, the remainder of the manuscript focuses on the observed seedling data and their relationship to expected seed accumulation as predicted by the mechanistic seed models.

These hypotheses were formalized statistically with generalized linear mixed effects models (GLMMs) which used seedling counts as the response variable and Patch ID as a random effect (Table 2) (glmer(); lme4; version 1.1–21; Bates et al., 2015). All predictor variables were scaled and centered before inclusion in models and the SNOW model was converted to a factor. The number of levels in the random effect (Patch ID) was lower than is

normally appropriate for a mixed effect model ($n = 3$) (Harrison et al., 2018). To ensure this was not causing major inaccuracies we also ran a series of generalized linear models (GLMs) with seedling counts as the response variable for each individual patch for a total of three model sets (referred to herein as "Single Patch Models") (Supplementary Tables S4 and S5 in Supporting Information S1). Due to the count nature of the response variables we used Poisson family or negative binomial responses in both the GLMMs and GLMs when it was necessary to account for overdispersion. Assumptions of GLM(M)s were visually inspected using simulated residuals (simulateResiduals(); 'DHARMa; version 0.2.7; Hartig & Lohse, 2020). Trigamma GLMM Pseudo-R^2s were calculated for the top models to determine model fit (r.squaredGLMM(); 'MuMIn'). Model-averaged coefficient estimates and 95% confidence intervals were calculated to assess the importance and effect size of each parameter included in each model set (Table 2). This method is recommended in order to reduce the need for arbitrary AIC thresholds and to clarify which terms in the model set are likely to have the greatest ecological importance (Anderson, 2008; Lukacs et al., 2010). We used the shrinkage method of model averaging to reduce overestimation due to model selection bias (Lukacs et al., 2010) and calculated the average using every model in the model set (Anderson, 2008). Variables were considered important if unconditional confidence intervals of the coefficient estimates did not cross zero.

2.5. Spatially Explicit Predictions of Sub-Basin Seedling Density (Question 3)

We selected the 95-ha Siksik Creek basin, a sub-basin of Trail Valley Creek (Figure 1) to assess the scalability of the mechanisms controlling seedling abundance addressed in Question 2. Values of all four accumulation models as well as TWI were calculated for 2,000 randomly selected points across the basin. Using the full model set of the seedling GLMM models (Table 2 and S3), we calculated a model-averaged prediction of seedling density for each of the 2,000 points (predict.averaging(); 'MuMIn'). These predicted point values were used to interpolate a surface of seedling density across the Siksik Creek basin using ordinary kriging. This was also done for the Single Patch Models (Figures S4 and S5 in Supporting Information S1).

2.5.1. Ground Validation of Seedling Density Maps

To validate the seedling density maps we randomly selected 51 points stratified by regions of high, medium, and low density that were predicted by the Single Patch Models (Figure S4 in Supporting Information S1). At each point, we recorded the distance to the third nearest alder seedling within a 5 m search radius. These points were then used to estimate the observed density and 95% confidence intervals for each stratum using the ordered distance method, a common field-based approach for measuring population densities (Krebs, 1998). These observed densities were then visually compared to the densities predicted by model extrapolation.

The performance of model extrapolations across the study basin was also assessed by converting the ordered distance data into seedling presence/absence. This was then used as a response variable in a model set of binomial family GLMs containing two models: a model with seedling density model extrapolations as an explanatory variable and a null model. All assumptions were visually assessed using 'DHARMa' (Hartig & Lohse, 2020) and Pseudo R^2 values were calculated using the r. squaredLR () function of the 'MuMIn' package.

2.6. Ground Cover Influence on Seedling Establishment (Question 4)

To assess the importance of microsite conditions on alder seedling establishment we determined the relative abundance of ground cover types (measured as percent cover) at the sub-plots described in the methods of Question 1. The ground cover types tested were selected either based on their dominance at the site or a priori evidence of their importance to tundra shrub recruitment. The resulting set of ground covers included: (a) *Sphagnum* spp. mosses, (b) non-*Sphagnum* mosses, (c) fruticose lichens (primarily consisting of *Cladonia* and *Stereocaulon* spp.), and (d) bare ground. This resulted in a data set of seedling counts and relative abundance of associated ground cover within 2 m^2 quadrats. We also selected a subsample of five of these sites for a more intensive survey of seedling density and the specific ground cover on which they were growing. Within this subsample we recorded the ground cover of every seedling encountered in a 2 m wide belt transect that ran parallel to the primary transect (offset by 3 m) and extended 20 m past the bottom patch edge.

To determine which ground cover type best supported alder recruitment we compared GLMM hurdle models of seedling abundance that used a Poisson response distribution, abundance of each ground cover type as predictors, and site as a random effect. The binomial model of the probability of zeros included ground cover as an

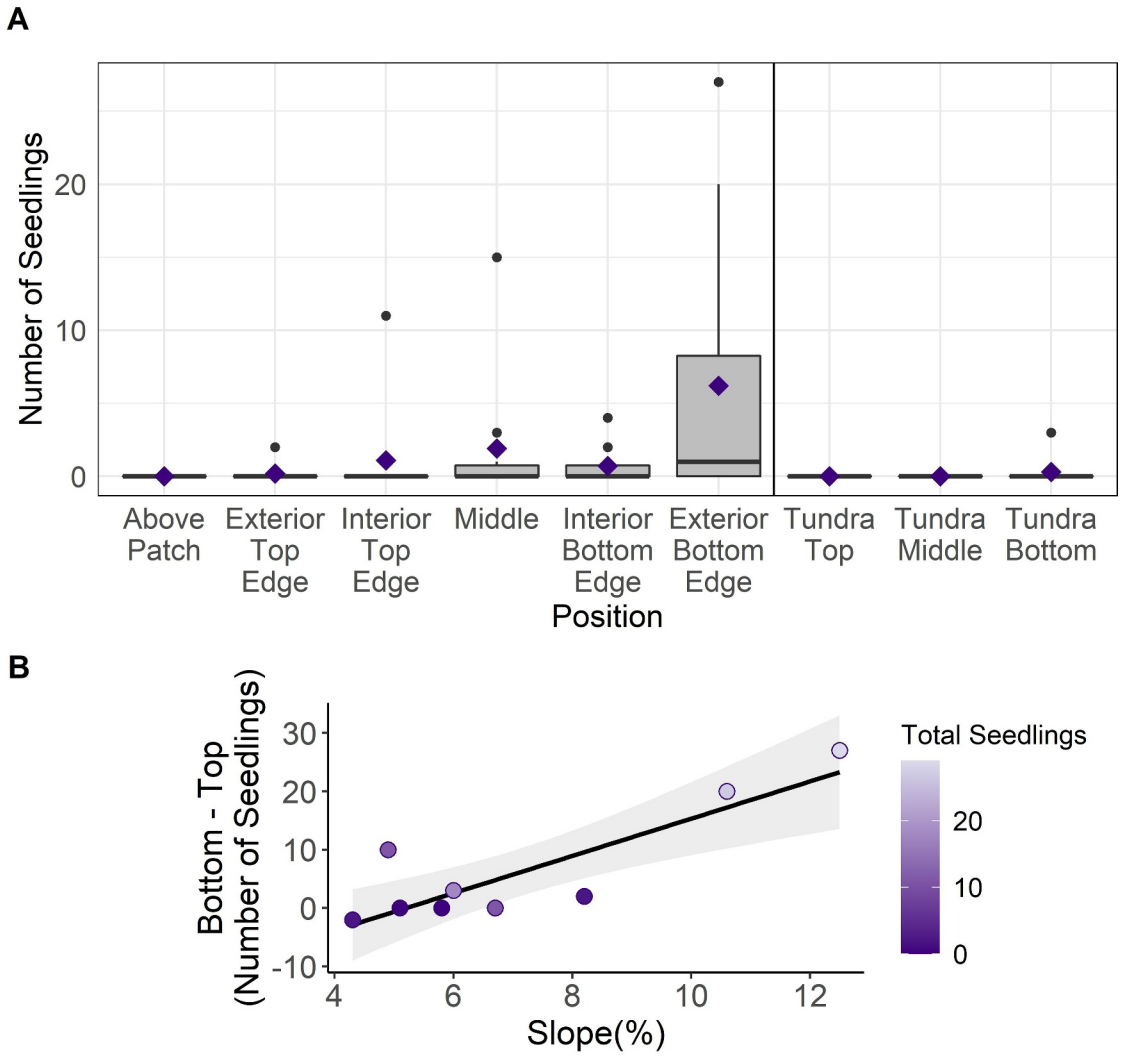

Figure 2. (a) Seedling counts by topographic position. Positions to the left of the vertical line indicate the transect through alder patches. Positions to the right indicate the transect through the alder-free tundra. Positions are progressively further down the hillslope moving from left to right within a transect. The horizontal black bars indicate the median and the purple diamond indicates the mean. (b) Difference in seedling count between Exterior Bottom Edge and Exterior Top Edge positions by steepness of hillslope ($R^2 = 0.52$). Positive values on the *y*-axis indicate greater recruitment at the Exterior Bottom Edge of the patch than the Exterior Top Edge, suggesting preferential downslope recruitment, while negative values represent the opposite. Color of points represent the total number of seedlings at each patch to distinguish between zeros caused by lack of seedlings and zeros caused by equal recruitment at top and bottom positions.

explanatory variable. Quadrats with outliers in the ground cover data were removed prior to modeling to avoid unrealistic model fits caused by lack of representation at higher cover values. Pseudo-R^2s were calculated to determine model fit (r2(); 'performance'). The intensive survey data was analyzed by calculating the proportion of seedlings at a site found in each ground cover and determining whether these proportions differed among ground cover types. This was done by comparing a general linear model with ground cover type as a predictor to a null model using the information-theoretic approach. Proportion of seedlings in a ground cover class per site was square root-transformed to meet assumptions of normality and homoskedasticity.

3. Results

3.1. Topographic Patterns of Recruitment (Question 1)

The evidence for a generalized trend of seedling abundance changing with topographic position through shrub patches was mixed as the model that included topographic position and the null model had similar probabilities

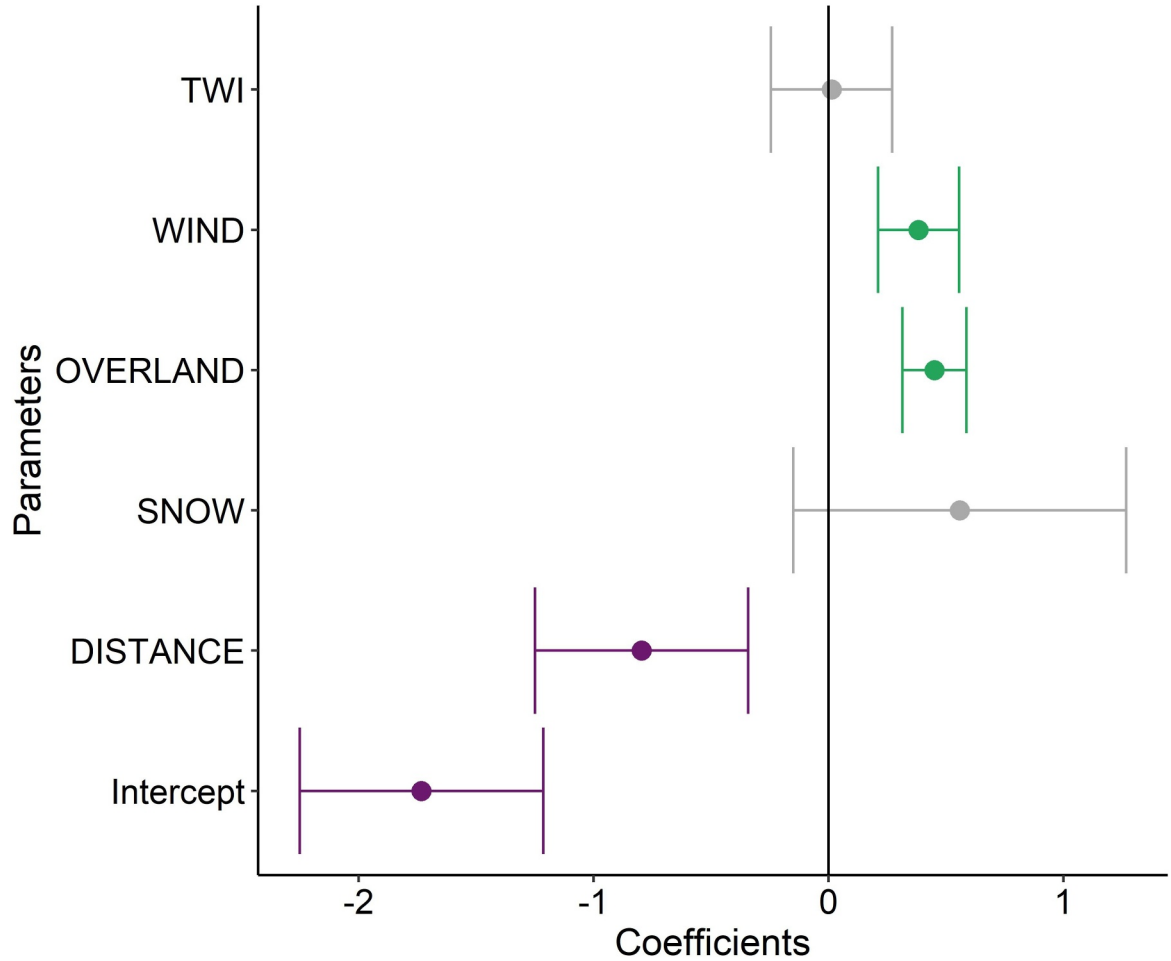

Figure 3. Model averaged parameter estimates for GLMM models of seedling density. Error bars represent 95% confidence intervals calculated using all models in the model set. Parameters represented are seed accumulation models of dominant wind direction (WIND), overland hydrochory (OVERLAND), snow drifting (SNOW), distance from seed sources (DISTANCE), and the model intercepts. Green points represent important positive model averaged estimates, purple points represent important negative estimates, and gray points represent unimportant terms.

of being the best model in the set (Figure 2a and Supplementary Table S6 in Supporting Information S1; w_i = 0.552 and 0.448 respectively). However, there were individual sites with clear preferential increases in seedlings at slope bottoms and these sites were associated with the steepest hillslope angles (>10%) (Figure 2b, Supplementary Table S7 in Supporting Information S1; top model w_i = 0.985, k = 2, where k is the number of models in a set, R^2 = 0.72). Seedlings were found in only one of 30 quadrats in the tundra transects (Figure 2a).

3.2. Fine-Scale Mechanisms Controlling Seedling Distributions (Question 2)

The model-averaged coefficients and 95% confidence intervals calculated using the full set of seedling models (Table 2 and S3 in Supporting Information S1) suggest OVERLAND, DISTANCE, and WIND were important predictors of seedling density (Figure 3b). Positive relationships were estimated between seedling density and all variables except DISTANCE. The seedling model with the greatest support (Seedling1; Table 2) included the variables OVERLAND, SNOW, DISTANCE, and WIND (w_i = 0.999, k = 16). The OVERLAND predictor occurred in the top three models (Table 2). The model with only DISTANCE (Seedling5; ranked 7th) and the null model (Seedling16; ranked 16th) both had Akaike weights of 0, indicating non-uniformity in the seedling recruitment patterns at these patches. Due to the low number of levels in the random effect "Patch ID", the best model (Seedling1) was unable to estimate variance associated with the random effect. Although the "Single Patch

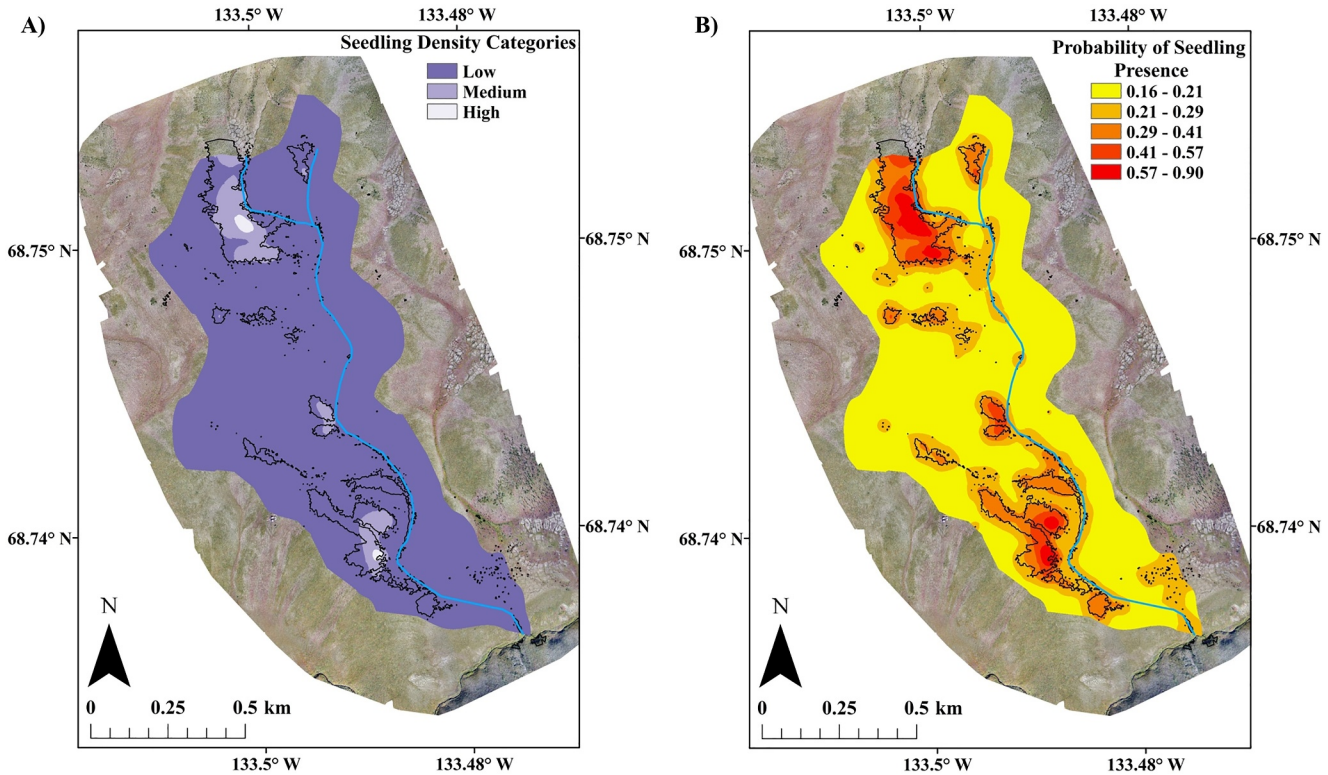

Figure 4. (a) Spatially explicit predictions of seedling density categories (Low = 0–0.23 seedlings/m^2, Medium = 0.23–0.46 seedlings/m^2, High = 0.46–0.69 seedlings/m^2) using model averaged coefficients. Model estimates were generated from 2,000 random points across the sub-basin and surface interpolation was performed using ordinary kriging of these points. Black polygons represent alder patches. The blue line represents Siksik Creek (b) Probability of alder seedling presence. Values were calculated using the fitted relationship between predicted seedling density and presence/absence observed at 51 validation points.

Models" of seedling density differed regarding which variables were considered most important, they largely corroborated the results of the models that included all patches (hereafter referred to as "All Patch Models") in that OVERLAND and DISTANCE were important predictors in two out of three patches (Text S2 in Supporting Information S1) as well as producing similar spatial predictions as discussed below. For these reasons, the remainder of this paper will focus on the results of the "All Patch Models" (see Text S2 in Supporting Information S1 for detailed justification, and Figures S4, S5, S6, and Tables S4, S5, S8 in Supporting Information S1 for results and relevant statistics associated with the Single Patch Models).

3.3. Spatially Explicit Predictions of Sub-Basin Seedling Density (Question 3)

Spatial patterns of predicted seedling density across the Siksik Creek sub-basin showed considerable clustering around mature alder patches (Figure 4). When compared to observed seedling data from across Siksik Creek, model predictions greatly over-estimated seedling density (Figure 5a). The relative ranking of predicted densities also did not align with the observed densities, though low and medium densities were distinct. However, the predicted seedling density did improve the explanation of observed presence/absence data relative to the intercept-only model (i.e., the overall odds of seedlings presence) (w_i = 0.996, k = 2, Pseudo-R^2 = 0.30, Figure 5b, Supplementary Table S9 in Supporting Information S1).

3.4. Ground Cover Influence on Seedling Establishment (Question 4)

The model of seedling abundance that included *Sphagnum* cover was more strongly supported than that of any other ground cover (w_i = 0.903, k = 6, R^2_m = 0.264; R^2_c = 0.992, Table 3). This model estimated a positive relationship between the average *Sphagnum* cover and the number of seedlings. The second most likely model estimated a negative relationship between seedling abundance and the cover of fruticose lichens, though the model weight was negligible (w_i = 0.097).

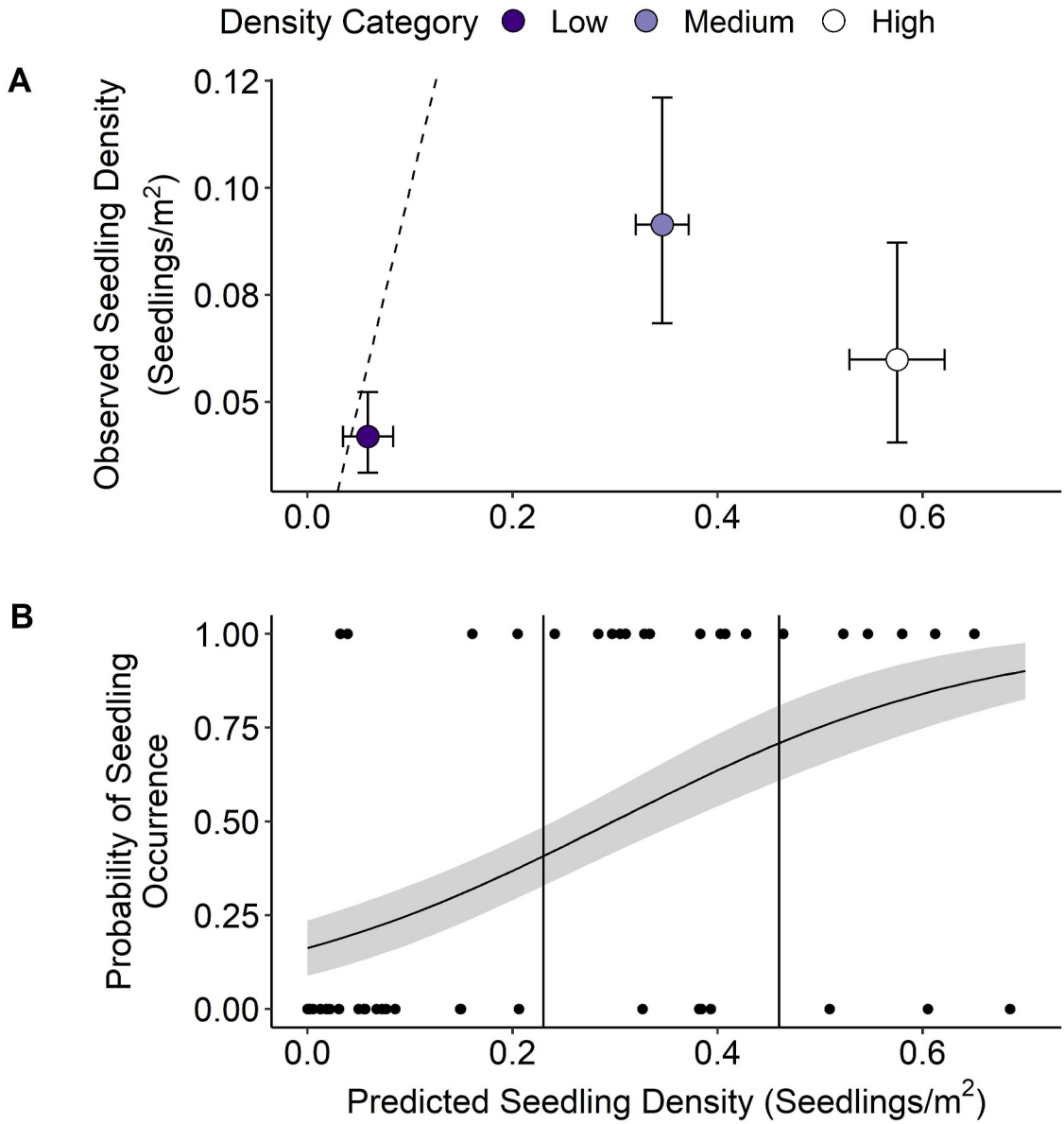

Figure 5. (a) Comparison of predicted and observed densities from 51 validation points across Siksik Creek sub-basin. Error bars represent 95% confidence intervals. Dashed line is the 1:1 relationship between observed and predicted densities. (b) Probability of seedling occurrence for given seedling densities predicted by the spatial model. Model fit by logistic regression (Pseudo-$R^2 = 0.30$). Shaded region represents standard error.

Seedlings were also found growing directly in *Sphagnum* most often (mean of 36% of seedlings per patch), though the proportion per patch was very similar for non-*Sphagnum* mosses (mean of 33% of seedlings per patch) (Figure S7 in Supporting Information S1). Only 3 seedlings out 565 (mean of 0.5% of seedlings per patch) were ever found growing in lichen ground cover. Comparison of a linear model which included ground cover as a predictor and a null model found the ground cover model to be most likely ($w_i = 1$, $k = 2$). These proportions differ considerably from the observed availability of ground cover types as lichen was the most abundant ground cover with a mean plot level abundance of 25.4%, followed by non-*Sphagnum* mosses (9.51%), *Sphagnum* spp (5.5%), bare ground (0.07%), and liverwort (0.05%).

Table 3
Model Set Used to Determine the Relative Importance of Different Microsite Ground Cover on Alder Seedling Abundance

Model	Log(L)	Δ AICc	w_i	Residual/null deviance	Residual/null df	Pseudo- R^2	
						Marginal	Conditional
Sphagnum cover	−67.553	0.00	0.903	135.1	79	0.264	0.992
Lichen cover	−69.784	4.46	0.097	139.6	79	0.555	0.994
Non-*Sphagnum* moss cover	−78.766	22.43	0	157.5	79	0.785	0.968
Null	−84.624	29.67	0	169.2	81	0	0.925
Bare ground cover	−83.893	32.68	0	167.8	79	0.396	0.943

Note. "Δ AICc" is the change in the corrected Akaike Information Criteria (AICc) between the target model and the next most likely model. "w_i" is model weight which gives the probability that the target model is the most likely model of the set. Model parameters in bold were estimated to have negative coefficients during model fit.

4. Discussion

The aim of this study was to investigate the mechanisms driving fine-scale spatial variability in alder shrub recruitment at the taiga-tundra ecotone of the Northwest Territories. Our data suggest that topographic position alone is not a strong predictor of seedling establishment and provide indirect evidence that spatial patterns of seed dispersal and accumulation play an important role in determining the heterogeneity of alder expansion at our study site. In particular, mechanistic models representing dispersal of seed via overland flow (OVERLAND), wind dispersal (WIND) and distance from the nearest alder patch (DISTANCE) best explained seedling densities. We propose that the most likely explanation of this observation is that localized seed limitation (i.e., increased seed availability leading to increased recruitment) is an important component in controlling fine-scale patterns of green alder recruitment at the taiga-tundra ecotone, though alternative explanations relating to environmental constraints are discussed below. If seed limitation is a dominant constraint, this is a novel finding and has important implications for the future spatial patterns of shrub expansion, most notably that recruitment responses to more favorable environmental conditions will likely depend on the quantity of seed arriving at a site. Recruitment success also differs as a function of seedbed quality; the cover of *Sphagnum* mosses was an important predictor of alder seedling abundance in alder patches, possibly due to increased water retention or decreased interspecific competition in *Sphagnum* mats. Taken together, our data suggest that both seed limitation and environmental constraints are important to consider when predicting the rates and extent of tundra shrub recruitment.

4.1. Fine-Scale Patterns of Seedling Distribution at the Taiga-Tundra Ecotone

Previous investigations of the fine-scale spatial heterogeneity of shrub expansion have found most expansion to be occurring at the bottom of slopes and other landscape positions that accumulate moisture (Naito & Cairns, 2011; Tape et al., 2006). Interestingly, our data suggest that the degree of preferential recruitment in low-lying positions at TVC likely varies among patches and is most pronounced where slopes are steepest (Question 1; Figure 2). One explanation of this pattern may be that overland hydrochory plays a role in constraining recruitment at the site, with steeper slopes having greater potential to transfer seed downslope. This explanation is supported by our investigation into the specific mechanisms of recruitment heterogeneity (Question 2) which indicates that locations with the greatest recruitment potential are those that are expected to receive seed via overland flow and are downwind of and near patches (Figure 3b and Table 2).

Spatial relationships between seed dispersal and seedling recruitment have been widely used in studies of plant demographics and community assembly to assess the relative magnitude of seed limitation across a site or landscape (Gratzer et al., 2022; Muller-Landau et al., 2002; Nathan & Muller-Landau, 2000; Norden et al., 2009). With some exceptions we discuss below, strong positive correspondence between seed and seedling abundance is generally interpreted as an indication that seed limitation is playing an important role in governing the spatial patterns of recruitment (Aicher et al., 2011; Nathan & Muller-Landau, 2000; Norden et al., 2009). The relationship between mechanistic models of seed accumulation (Table 1) and measured seedling recruitment reported here therefore suggests that seed limitation controls an important component of recruitment variability at TVC, as places with greater expected seed input coincide with greater seedling abundance (Nathan & Muller-

Landau, 2000; Norden et al., 2009) (Figure 3b). It is possible that this pattern was caused by disproportionate seed arrival to suitable microsites (i.e., directed dispersal) which can result in false positive indications of seed limitation (Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995). We consider this unlikely however given the abundance of unsuitable lichen microsites throughout the modeled seed shadows.

If seed limitation is a major control on recruitment patterns at TVC, there are likely locations across the landscape that could support seedlings that do not receive seed as well as locations that receive seed but remain seed limited because of insufficient seed input. This may explain why environmentally similar locations can display very different recruitment patterns at the same site (e.g., Bottom Patch Exterior and Tundra Bottom quadrats; Figure 2a) as seeds are likely not reaching the alder-free tundra transects. This argument is further strengthened by the observation from previous work at the site that *Sphagnum* spp. - found here to be an important substrate for recruitment - are as abundant in alder-free tundra as they are in patches (Wallace & Baltzer, 2020), suggesting spatial variability in the capacity for suitable microsite colonization.

The potential for seed limitation at TVC is ecologically significant because it suggests that the factors that control seed dispersal patterns (e.g., dominant wind directions or snow drift locations) influence seedling distribution alongside those that govern seedling establishment and survival (e.g., site quality, temperature, or herbivory) and these factors may exhibit different sensitivities to climate change. For example, an increase in air temperature may increase seed viability rates (Lantz et al., 2010) but may also alter the patterns of accumulation mechanisms themselves due to changes in wind patterns (Gearheard et al., 2009; Mioduszewski et al., 2018) or snowpack conditions (Brown et al., 2010), thereby altering the likelihood of seed arrival for any given location across the landscape. This may lift or impose localized seed limitation and result in very different spatial patterns of shrub expansion than we would expect from a response due solely to changing environmental conditions.

Our interpretation of these results as evidence of seed limitation relies on the assumption that the mechanistic models realistically represent spatial patterns of seed dispersal and do not simply covary with environmental gradients which drive the recruitment response. While the seed trap data had been collected in an effort to validate the mechanistic models, our *post hoc* discovery that the traps did not capture overland flow processes makes it difficult to use the data in this manner. Regardless we argue that the mechanistic models as represented here are unlikely to correspond to environmental factors which dominate alder recruitment and productivity. The OVERLAND and WIND models for example, do not represent catchment size, water flow, or windspeed themselves but rather the number of shrub patch pixels in the contributing area of a target point (Table 1). Therefore, any potential environmental covariate would need to be a function of both alder cover and connectivity to that cover, likely limiting the number of possible covarying factors. In the case of OVERLAND, we suspect the most likely environmental covariate would be inorganic leaching of nitrogen resulting from nitrogen fixation (Salmon et al., 2019). While hydrological connectivity to alder patches has been suggested to be an important determinate of downslope nitrogen availability at a study site in Alaska (McCaully et al., 2022), previous work at TVC found no evidence of increased inorganic nitrogen availability or foliar nitrogen concentrations directly downslope of alder patches (Black et al., 2021; Wallace & Baltzer, 2020), suggesting the potential of this mechanism to drive recruitment patterns at TVC is minimal. We suggest therefore that the simplest explanation is that OVERLAND predominantly captures overland hydrochory and seed dispersal rather than nitrogen availability or other environmental conditions.

Despite not capturing overland hydrochory processes, the seed trap data do provide some additional support to the hypothesized importance of seed limitation at TVC. The seed traps, which likely capture pre-melt seed distribution accurately, indicate a strong decrease in seed density as a function of distance from the patch edge, with little to no seed observed past 35 m (Figure S9 in Supporting Information S1). This suggests that even in the absence of post-melt redistribution by overland hydrochory, alder seed dispersal at the site is highly spatially constrained, with large fractions of the landscape receiving no seed. While this alone is not direct evidence of seed limitation without information about suitable microsite availability, we consider it unlikely that all environmentally suitable microsites fall within 35 m of alder patches, particularly given the abundance of *Sphagnum* spp. at the site (Wallace & Baltzer, 2020).

Although the SNOW mechanistic seed model was included in the top ranked statistical model of seedling density (Table 2), it was not found to be an important driver of seedling recruitment patterns at TVC (Figure 3). Snow plays a critical role in shaping spatial variability in tundra communities (Walker et al., 2000). Drifts formed during blowing snow events develop around topographic depressions as well as tall shrub patches (Marsh &

Pomeroy, 1996; Sturm et al., 2001). The accumulated snow acts to increase subnival soil temperature and protect vegetative buds from desiccation (Ray & Bret-Harte, 2022; Sturm et al., 2001). As a result, microsite variability in snow depth can have a strong impact on plant community composition and function (Niittynen, Heikkinen, & Luoto, 2020; Niittynen, Heikkinen, & Luoto, 2020). Despite these factors complicating the interpretation of the SNOW model as solely a proxy for seed dispersal, we note that the seed trap data were explained well by the statistical model which included both SNOW and DISTANCE (Table S1 in Supporting Information S1; $R^2_m = 0.275$; $R^2_c = 0.317$). This suggests that snow drifting does appear to play a role in pre-melt seed accumulation patterns. The limited importance of the SNOW model on seedling recruitment may simply be the result of overland hydrochory and subsequent transport of seed away from snow drifts during melt. Such a hypothesis is beyond the scope of this work however and warrants further study.

The limited importance of TWI as a predictor of recruitment heterogeneity (Figure 3b) in addition to the complex pattern of recruitment as it relates to hillslope position (Figure 2) suggest that topographic resource gradients play a weaker, or less consistent, role in governing alder recruitment at this site than observed elsewhere (e.g., Naito & Cairns, 2011; Tape et al., 2006). Our observations are consistent however with recent work from the broader region surrounding TVC which found species distribution models of mature alder to be generally insensitive to TWI (Seider et al., 2022). These findings, as well as the indirect evidence for localized seed limitation suggest that a more constrained zone of potential expansion exists at our study site than observed in other regions and that the magnitude of future alder colonization and infilling will vary among downslope locations. One reason for this divergence between our study site and those with strong expansion-TWI relationships may be related to a weaker relationship between TWI and resource availability at TVC. For example, sites in the Brooks Range of Alaska (e.g., Naito & Cairns, 2011; Tape et al., 2006, 2012) generally have greater topographic relief and are more incised than our study region (Fraser et al., 2014). As such the range of TWI values observed is considerably lower than those reported from the Brooks Range (e.g., Naito & Cairns, 2011), possibly explaining the lack of downslope nutrient and moisture gradients at the site (Black et al., 2021; Wallace & Baltzer, 2020).

4.2. Ground Cover Type as an Environmental Constraint on Recruitment

While TWI did not explain variability in alder recruitment, we did find evidence that environmental conditions play an important role in governing seedling abundance by way of a clear association between recruitment and the abundance of *Sphagnum* mosses (Table 3 and Figure S8 in Supporting Information S1). *Sphagnum* mats are typically nutrient poor and can outcompete vascular plant species for mineral nutrient inputs (Heijmans et al., 2002; Malmer et al., 2003). It is possible that alder seedlings can take advantage of decreased vascular plant cover in these mats owing to their capacity for nitrogen fixation (Densmore, 2005). Furthermore, *Sphagnum* species retain moisture very effectively during drought (Shetler et al., 2008) which may decrease drought stress for developing seedlings. Previous studies have documented increased alder recruitment in disturbed mineral soils (e.g., Frost et al., 2013; Lantz et al., 2013; Tremblay et al., 2012). The data presented here complement this previous work by suggesting that recruitment remains variable among ground cover types in the absence of disturbance and that, in addition to disturbance, spatial variation in *Sphagnum* abundance may be an important predictor of recruitment heterogeneity. Considering the indirect evidence of seed limitation presented in this study, we suggest that both *Sphagnum* microsite and seed availability are likely important constraints to recruitment at this site.

4.3. Sub-Basin Scale Extrapolation of Seedling Model

The extrapolated model averaged predictions of seedling density were relatively successful at predicting observed seedling presence/absence across the Siksik Creek basin (Figure 5b). Therefore, the resulting map provides a reasonable prediction of zones of potential alder shrub expansion in the sub-basin (Figure 4). Recruitment outside of these zones is expected to be minimal, while recruitment inside will depend on the strength of environmental limitations. Based on this map, most of the areas expected to be medium and high density occurred near or within existing patches (Figure 4). This is likely due to the importance that DISTANCE played in the seedling model set (Figure 3b) as well as the generally small catchment areas of the points calculated for the OVERLAND model. The limited dispersal predicted here may provide another potential explanation for previous studies showing that one of the strongest predictors of expansion is the presence of existing shrub patches (Lantz et al., 2013; Lemay et al., 2018). Importantly, previous work from the broader region around TVC found that within sampling plots (radius of 15 m) alder recruits displayed a

random spatial pattern with respect to mature individuals, suggesting that at this scale there was no evidence of dispersal limitation or aggregation around mature individuals (Travers-Smith & Lantz, 2020). Given the results of this study, our findings suggest that seedlings at TVC may aggregate, not at the scale of mature alder individuals, but rather at the scale of alder patches. It is unclear to what extent this observation extends to the remainder of the region however, as alder density is relatively low across the landscape at TVC (Lantz et al., 2013) and dispersal from a patch may become less important with greater alder densities. Overall, our results suggest that future expansion may be dominated more by patterns of increased alder density within patches than by large increases in the areal extent of alder patches. The magnitude of density increases in the predicted high-density zones will likely depend on the degree of competition experienced within patches. Previous work in Alaska has demonstrated that alder distributions can be strongly controlled by nitrogen competition (Chapin et al., 1989) though the importance of this process in our study region requires further investigation.

4.4. Seed Limitation and Future Predictions of Shrub Recruitment

Based on several lines of evidence presented here, we suggest that spatial patterns of both seed limitation and ground cover play an important role in governing fine-scale variability of shrub recruitment in tundra systems. Our results also suggest that accurate prediction of seedling density may be improved by considering slope steepness. An important deficit of this study is the assumption made by the statistical models and mapping that all locations have the capacity to be seed limited. This is unlikely to be true given the ground cover data, in that, for example, lichen cover was not a viable option for seedling recruitment (Figure S7 in Supporting Information S1). Future predictions of seedling density would be improved by identifying suitable microsites within zones of high seed accumulation. This could likely be achieved with careful deployment of seed addition experiments (Turnbull et al., 2000).

In addition to considerations of seed arrival, inclusion of seed viability in efforts to forecast shrub expansion may also be important. Green alder displays strong positive relationships between seed viability and mean annual temperature (Lantz et al., 2010). If climate warming increases both viable seed production and the regional rates of seedling survival, the relationship between seed accumulation mechanisms and seedling density may decrease in importance over time because even in zones of low seed input, the likelihood of seedling establishment will increase. Alternatively, if seedling survival rates increase without increases in seed viability, we would expect the importance of seed accumulation to increase, as survival would become more likely inside zones of high input with minimal change in low input zones. The importance of seed accumulation mechanisms in predicting shrub recruitment may also vary across space, with some study sites and regions having greater seed viability, and therefore potentially less seed limitation than others. Because our study site has relatively low alder density (Lantz et al., 2013) and seed viability (Lantz et al., 2010) and has experienced smaller increases in vegetation productivity relative to other areas of the study region (Fraser et al., 2014) we may expect the relationships between seed accumulation mechanisms and seedling recruitment to be stronger here than other sites. How our results extend to sites and regions with higher viability, greater increases in productivity, and denser populations is currently unknown but warrants further investigation.

Taken together, the results reported here suggest a complex pattern of shrub recruitment which differs from observations from other study regions. In particular, the potential for seed limitation as a mechanism of recruitment heterogeneity is a novel finding and may have important consequences for the rates and magnitude of shrub expansion. In conjunction with the observed relationships between recruitment and *Sphagnum* abundance, these data suggest that consideration of both seed arrival and environmental suitability may improve our capacity to predict spatial patterns of shrub expansion in tundra environments. Such predictions are important to understanding the magnitude of change to ecosystem function and interactions between the biosphere and the atmosphere we will expect in a shrubbier Arctic.

Data Availability Statement

The data and analytical code (Wallace et al., 2024) used in this study are available at Borealis via https://doi.org/10.5683/SP3/UJVZ9I.

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