1	Insights into the tussock growth form with model data fusion				
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22 Summary:

- Some rhizomatous grass and sedge species form tussocks that impact ecosystem structure and
 function. Despite their importance, tussock development and size controls are poorly
 understood due to the decadal to centennial timescales over which tussocks form.
- We explored mechanisms regulating tussock development and size in a ubiquitous arctic
 tussock sedge (*Eriophorum vaginatum* L.) using field observations and a mass balance
 model coupled with a tiller population model. Model data fusion was used to quantify
 parameter and prediction uncertainty, determine model sensitivity, and test hypotheses on
 the factors regulating tussock size.
- The model accurately captured the dynamics of tussock development, characteristics, and size observed in the field. Tussock growth approached maximal size within several decades,
 which was determined by feedbacks between the mass balance of tussock root necromass and density-dependent tillering. The model also predicted that maximal tussock size was primarily regulated by tiller root productivity and necromass bulk density and less so by tiller demography. These predictions were corroborated by field observations of tussock biomass and root characteristics.
- The study highlights the importance of belowground processes in regulating tussock
 development and size and enhances our understanding of the influence of tussocks on arctic
 ecosystem structure and function.

41 **1. Introduction**

42

Rhizomatous grass and sedge species often form clumps of individual tillers that result in the 43 formation of tussocks (Wein, 1973; Oliva et al., 2005; Lawrence & Zedler, 2011; Derner et al., 44 2012). Tussock-forming species are often considered ecosystem engineers or foundation species 45 and influence a variety of ecosystem properties, including micro-topography, soil moisture, soil 46 carbon (C) accumulation, and species diversity (Crain & Bertness, 2005; Peach & Zedler, 2006; 47 Benscoter & Vitt, 2008; Varty & Zedler, 2008; Eldridge et al., 2010; Balke et al., 2012; 48 Elumeeva et al., 2017; Qiao et al., 2020). This is especially true in the Arctic, where tussock 49 cottongrass (Eriophorum vaginatum L.) forms elevated mounds of root necromass as a strategy 50 to escape the poor growing conditions of waterlogged anoxic soils (Fig. 1) (Chapin et al., 1979; 51 Crain & Bertness, 2005; Lawrence & Zedler, 2011). Tussocks enhance arctic soil organic C 52 stocks and have exhibited declines in abundance in some areas in response to recent climate 53 change (McGraw et al., 2015; Hobbie et al., 2017; Box et al., 2019; Curasi et al., 2022; 54 Macander et al., 2022). These declines are concerning since climate change has the potential to 55 56 alter tussock formation, size, and abundance resulting in large regional losses and gains in arctic C stocks (Curasi et al., 2022). 57

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Much of our understanding of E. vaginatum tussock formation is based on qualitative 59 60 observations and demographic models that exclude the necromass that provides the structure on which tillers reside (Fetcher & Shaver, 1982; Fetcher & Shaver, 1983; Mark et al., 1985; Shaver 61 62 et al., 1986; Bennington et al., 2012; McGraw et al., 2015). The exclusion of the links between necromass, tiller demography, and tussock C storage potential limits our ability to predict 63 64 climate change impacts on tussocks (Bennington et al., 2012; McGraw et al., 2015; Curasi et al., 2019; Curasi et al., 2022). Tussocks are formed by a population of interconnected asexually 65 propagating tillers that reside on an elevated surface created by the accumulation of root 66 necromass and litter (Wein, 1973; Chapin et al., 1979; Mark et al., 1985). Tussocks have both 67 above and belowground components, with their total mass being related to their diameter through 68 allometric constraints on size and growth (Chapin et al., 1979; Curasi et al., 2022). The diameter 69 of E. vaginatum tussocks rarely exceeds 50 cm, which suggests that there are limits to their 70 maximum size and C storage potential (Fetcher & Shaver, 1982; Fetcher, 1983; Mark et al., 71

1985). Tussocks develop over decades to centuries, with estimated ages for mature tussocks

between 122 and 187 years based on tiller growth and turnover (Wein, 1973; Chapin *et al.*, 1979;

74 Mark *et al.*, 1985). Tussock's long lifespan (i.e., decades to centuries) challenges our ability to

violation regulate their formation, size, and C storage potential (Fetcher &

76 Shaver, 1982; Mark *et al.*, 1985; Oliva *et al.*, 2005; Lawrence & Zedler, 2011; Lawrence &

77 Zedler, 2013). This is unfortunate given their prominent role as a foundation species in the Arctic

and hence their importance in predicting the ecosystem's response to climate change.

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E. vaginatum tussocks are considered foundational because of their disproportionate impact on 80 ecosystem properties, C fluxes, and C stocks in moist acidic tundra ecosystems (Wein, 1973; 81 Oberbauer et al., 2007; Curasi et al., 2022). In moist acidic tundra ecosystems, E. vaginatum 82 tussocks can account for up to one-third of primary productivity, and their necromass C can 83 enhance soil organic layer C stocks by up to 30% (Chapin & Shaver, 1985; Curasi et al., 2022). 84 This is a product of *E. vaginatum*'s high allocation of biomass belowground, with belowground 85 to above ground biomass ratios that are 3-7 times higher than other tundra species (Iversen *et al.*, 86 2015; Curasi et al., 2022). Tussocks have declined in abundance in response to historical climate 87 change and may continue to decline into the future, ultimately impacting tundra C stocks 88 (McGraw et al., 2015; Hobbie et al., 2017; Box et al., 2019; Curasi et al., 2022; Macander et al., 89 2022). Our limited understanding of the tussock growth form prevents us from explicitly 90 91 representing its unique characteristics and C cycling impacts in terrestrial biosphere models (TBMs). Currently, terrestrial biosphere models characterize tundra vegetation as a single or a 92 93 limited number of plant functional types (PFTs), including non-tussock forming C3 grasses or sedges. However, they do not explicitly represent the tussock growth form with its highly 94 95 productive root system and large necromass C pool (Epstein et al., 2001; Dorrepaal, 2007; Sullivan et al., 2007; Wullschleger et al., 2014; Iversen et al., 2015; Mekonnen et al., 2021). 96 Given tussocks' unique and important role in C storage in tundra ecosystems, their exclusion 97 could result in non-linear predictive biases in TBMs that have implications for future C Arctic 98 cycling predictions (Epstein et al., 2001; Dorrepaal, 2007; Fisher et al., 2014; Saccone et al., 99 2017; Fisher et al., 2018; Huntzinger et al., 2020; Mekonnen et al., 2021). Hence, improving our 100 understanding of the tussock growth form will allow for a more realistic representation of 101 tussocks within TBMs that will improve future arctic C cycle projections (Curasi et al., 2022). 102

104	We hypothesize that tussock formation and size are controlled by three main types of factors:
105	physical, structural, and demographic. Physical factors directly contribute to tussock C storage
106	and include root production that increases tussock size as well as the decomposition of root
107	necromass and dead tillers that reduces tussock size (Chapin et al., 1979; Curasi et al., 2022). In
108	the Arctic, E. vaginatum has a deciduous root system that produces and accumulates
109	considerable necromass to form the tussock mound (Chapin et al., 1979; Ma et al., 2022).
110	Structural factors directly relate to a tussock's structural composition and include the root
111	necromass bulk density and the size of the tillers that reside atop the tussock. Necromass
112	comprises a majority (\sim 70%) of total tussock mass, and its bulk density (g cm ⁻³) determines the
113	amount of root necromass required to "build" a tussock of a given volume (Curasi et al., 2022).
114	Tiller size is a structural factor that determines the maximal density of tillers that reside atop a
115	tussock (Fetcher & Shaver, 1982). Demographic factors are associated with the per-capita
116	tillering rate, initial per-capita death rate, and initial per-capita population growth rate of the
117	living tillers that reside atop the tussock (Fetcher & Shaver, 1983; Bennington et al., 2012;
118	McGraw et al., 2015). Here, we present a parsimonious tiller population model coupled with a
119	mass balance model and determine the relative importance of these factors in determining
120	tussock size and tussock C stocks. The model predictions were constrained with field
121	measurements of tussock allometry, tiller characteristics, and tiller demography through model-
122	data fusion using a Monte Carlo algorithm to predict model parameters.
123	

- **2. Materials and methods**

2.1 Philosophy of approach

Parsimonious mathematical models are widely used for prediction and hypothesis testing in
ecology and evolutionary biology, especially for long-term processes that are difficult to measure
(Dietze *et al.*, 2013; Rastetter, 2017; Kyker-Snowman *et al.*, 2022). The strength of a
parsimonious model is its tractability, while its weakness lies in its inability to represent every
process, which may decrease a model's predictive value (Rastetter, 2017). Parsimonious model
validation is often performed through comparison with observations; however, these
comparisons do not account for the impacts of observation parameter uncertainty on model

134 predictions. Recently, statistical techniques have been developed to constrain model predictions and determine prediction uncertainty through the use of model-data fusion (Keenan et al., 2011; 135 136 Zobitz et al., 2011). Model data fusion using a Monte Carlo algorithm statistically constrains model parameters, so that model predictions closely match observations provided their 137 uncertainty (Keenan et al., 2011; Peng et al., 2011; Keenan et al., 2012; Wright & Rocha, 2018). 138 Because model data fusion is iterative, it also can determine a model's sensitivity to parameter 139 changes, providing insight into the importance of various model processes in making predictions 140 (Peng et al., 2011; Zobitz et al., 2011; Wright & Rocha, 2018). Here we use model data fusion 141 alongside a newly developed parsimonious model of tussock formation to determine the relative 142 importance of physical, structural, and demographic factors in determining tussock size and 143 tussock C stocks. 144

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146 2.2 Temporal and spatial variability of in situ tussock size

We measured the spatial and temporal variability in tussock size to assess size controls and 147 temporal changes (Fig. S1). To quantify spatial variability in tussock size, we measured the 148 diameter and height above the moss surface of 2,321 tussocks across 46 sites along a latitudinal 149 gradient across the North Slope of Alaska. Tussocks were selected for measurement if their 150 centers intercepted a 200 m transect tape at each site. For each tussock, two perpendicular 151 measurements of diameter were taken using tree calipers, and four measurements of height above 152 153 the moss surface were taken with a ruler in each cardinal direction. To quantify the temporal change in site average tussock size, we repeated tussock diameter measurements at four sites that 154 were surveyed in the late 1970s in 2016/2018 (Fetcher & Shaver, 1982). One site (Eagle creek 155 bladed, EC-B) was cleared by a bulldozer in 1977 and represented a disturbed site with young 156 157 developing tussocks. The other three sites (Eagle creek undisturbed EC-U and Cape Thompson 1/2) had no recorded history of disturbance since 1970 and represented mature tussocks. Tussock 158 159 diameters were averaged per site and period and related to climate and height using linear regression. Climate data were obtained from WorldClim 2 and extracted using each site's GPS 160 161 coordinates (Fick & Hijmans, 2017).

164 Tussocks were harvested during the peak of the growing season in 2016 at the Toolik Lake LTER site (n = 35) to quantify tussock allometry, tiller characteristics, and decomposition. For 165 tussock allometry, we measured tussock mass, diameter, height above the moss surface, and total 166 above and belowground height. Tussock mass was separated into tiller leaf litter, brown/black 167 root necromass, green living tillers, and white live roots. Bulk density was quantified from the 168 dry weight of root necromass within a cylindrical core of known volume (5.7 cm diameter and 169 170 \sim 30 cm long) taken through the center of each tussock. For tillers, we measured the number of living and dead tillers, annual tiller root production, living and dead tiller diameter, and tiller 171 propagation rates for each harvested tussock. Tiller propagation was estimated as the number of 172 newly developed secondary tillers without developed leaves divided by the number of living 173 adult tillers. Tussocks were measured by taking two perpendicular measurements using tree 174 calipers for diameters and four measurements using rulers for lengths. Tillers were measured by 175 taking a single measurement at their base using calipers. All mass measurements were taken after 176 oven-drying the material at 60 °C for 48 hours. Samples of tussock root necromass (n = 76) and 177 dead tillers (n = 15) were set aside for a decomposition experiment using the mesh-bag technique 178 (Karberg et al., 2008). For each sample, ~5 g of dry material was weighed, sealed in a mesh bag, 179 and reweighed after a year in the field. The annual mass change in each mesh bag was used to 180 estimate negative exponential decay constants using methods described by Parker et al. (2018) 181 and Andren and Paustian (1987). 182

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184 *2.4 Tussock Size Model*

We developed a model for individual tussocks using a series of coupled differential equations describing tiller population dynamics and tussock mass balance (Fig. 2). The model represented an individual tussock as a root necromass island that supported a population of living and dead tillers. The tussock island changed volume (V; cm³) according to modeled changes in root necromass (ΔM : g y⁻¹) and average root necromass bulk density (ρ ; g cm⁻³) (Eqn. 1).

$$\frac{dV}{dt} = \frac{\Delta M}{\rho}$$
 Eqn. 1

191 Representing the tussock as a volume allowed for the relationship between tussock height and tussock radius to be defined using a 3-dimensional shape. We used the necromass bulk density, 192 193 tussock radius, and tussock necromass measurements described in section 2.3 to fit an allometric relationship (i.e., tussock radius vs. necromass) using four common three-dimensional shapes: 194 195 inverted cone, half-sphere, cylinder, and modified cylinder. The tussock shape was determined before model parameterization to avoid parameter identifiability and equifinality issues during 196 197 model-data fusion (Beven, 2006; Keenan et al., 2011; Peng et al., 2011). Out of the four commonly used three-dimensional shapes, the modified cylinder minimized the mean absolute 198 error between modeled and measured allometry (Fig. S2a). The representation of a tussock as a 199 modified cylinder indicates that changes in tussock radius are accompanied by linear changes in 200 201 height. This was supported by measurements that demonstrated strong linear correlations between tussock radius and height above the moss surface ($y = 0.004 \pm 0.05 + 1.03x \pm 0.02$, P < 202 0.001, $R^2 = 0.55$), and tussock radius and total tussock height ($y = 9.09 \pm 1.5 \pm 1.52x \pm 0.16$, P < 203 0.001, $R^2 = 0.73$) (Fig. S2b). Given this geometry, tussock radius at time t (r(t); cm) was related 204 to M at time t, ρ , and the fitted ratio between tussock height and radius (1.6) with Eqn. 2. 205 206

$$r(t) = \sqrt[3]{\frac{M(t)}{1.6\pi\rho}}$$
 Eqn. 2

207

A tussock supports a total population (N_T ; number of tillers) of living (N_A ; number of tillers) and dead (N_D ; number of tillers) tillers that occupy the top of the tussock (Eqn. 3).

210

$$N_T = N_A + N_D$$
 Eqn. 3

211

The change in the population of N_A was represented with a logistic growth model using an initial per-capita growth rate $(r_A; y^{-1})$ and a carrying capacity for live tillers (K_A ; number of tillers) (Eqn. 4).

$$\frac{dN_A}{dt} = r_A N_A \left(1 - \frac{N_A}{K_A} \right)$$
 Eqn. 4

229

217 This representation of the living tiller population dynamics implements density-dependent 218 tillering rates, which is supported by observed declines in tillering rates as tussocks mature (Fetcher & Shaver, 1982; Fetcher, 1983; Fetcher & Shaver, 1983). Density-dependent tillering is 219 220 common in rhizomatous grasses as it reduces intraspecific competition and tiller overproduction (Antonovics & Levin, 1980; Barkham & Hance, 1982; Lonsdale & Watkinson, 1983; Fetcher, 221 222 1985; de Kroon & Kwant, 1991; de Kroon, 1993). Tiller mortality was modeled as being density independent because density-dependent mortality has been shown to be nonexistent or weak in 223 rhizomatous plants (de Kroon & Kwant, 1991; de Kroon, 1993). K_A was determined by the space 224 atop the tussock for new tillers that was unoccupied by living and dead tillers. The total number 225 of tillers that a tussock can support at time t ($\eta(t)$; number of tillers) was determined with a 226 hexagonal packing model where tillers of an average diameter (θ ; cm) optimally fill a circular 227 area defined by the tussock radius at time t (Eqn. 5). 228

$$\eta(t) = \frac{\pi r(t)^2}{\theta^2 \sqrt{12}}$$
 Eqn. 5

230 Hexagonal packing is common in clonal plants and organismal structures (i.e., honeycombs) and serves as a way to maximize packing density in a given area (Darwin, 1859; Bell, 1979; 231 Wolfram, 2002; Stephenson, 2003; Oborny et al., 2012; Nazzi, 2016). Hexagonal packing on a 232 circular area (Eqn. 5) was able to capture the total tiller population in harvested tussocks 233 described in section 2.3 with a mean average percent error of 17% (Fig. S3), validating the use of 234 hexagonal packing in the model. To demonstrate the role of tiller packing on tussock 235 development, we derived the packing index as the ratio between η and $N_T (N_T/\eta)$. A packing 236 index of 1 indicates insufficient space for new tillers, whereas a packing index of less than 1 237 indicates sufficient space for new tillers. K_A was calculated using Eqn. 6. 238 239

$$K_A(t) = \eta(t) - N_D(t)$$
 Eqn. 6

The change in the population of N_D was a function of gains from the death of live tillers ($d_A * N_A$; number of tillers y⁻¹) and losses from the decomposition and removal of dead tillers atop the tussock $(k_D * N_D;$ number of tillers y⁻¹) (Eqn. 7). d_A (y⁻¹) was the initial per-capita death rate for live tillers that contributed to the dead tiller population, and k_D (y⁻¹) was the dead tiller decomposition and removal rate for dead tillers that make space for new tillers to form atop the tussock.

246

$$\frac{dN_D}{dt} = \overbrace{d_A N_A}^{Gains} - \overbrace{k_D N_D}^{Losses}$$
Eqn. 7

The mass balance of *M* was a function of the root necromass added to the tussock by live tillers ($\alpha * N_A$; g y⁻¹) and root necromass losses via decomposition ($k_M * M$; g y⁻¹) (Eqn. 8). α was the root input rate per tiller (g tiller⁻¹ y⁻¹) that adds mass and volume to the tussock, and k_M was the decomposition rate of root necromass (y⁻¹) that removed mass and volume from the tussock.

$$\frac{dM}{dt} = \frac{Gains}{\alpha N_A} - \frac{Losses}{k_M M}$$
 Eqn. 8

The model had seven parameters that determined tussock development and size (Table 1). Physical factors were associated with α , k_M , and K_D , structural factors were associated with θ and ρ , and demographic factors were associated with r_A and d_A . We used fitted parameters to calculate the per-capita tillering rate (b) using Eqn. 9, which was derived through algebraic

256 manipulation of Eqn. 4 when population growth was at steady state (methods S1; Fig. S4).

$$b = d_A + r_A \left(1 - \frac{N_A}{K_A} \right)$$
 Eqn. 9

Given the strong coupling between tussock mass balance, volume, and available space for tillers, we hypothesized that physical factors would primarily determine steady-state tussock size. The tussock size model was solved for 250 years at a three-month time step numerically in R using the Runge-Kutta fourth-order method in the "deSolve" package (Soetaert *et al.*, 2010; R Core Team, 2019). It was parameterized using the model data fusion routine described in the next section (2.5).

263

264 2.5 Model parameterization with model-data fusion

265 Our tussock model was parameterized using a weighted least-squares two-step model-data fusion based on Keenan et al. (2012), Richardson et al. (2010), and Wright and Rocha (2018). The 266 267 uniform prior distributions for ρ , θ , α , and k_M were based on the maximum and minimum values observed in the field (Table 1). Relatively few samples of dead tiller decomposition were 268 available in the field data; however, the available samples fell within the same range as the root 269 necromass decomposition rates. Therefore, the uniform bounds for k_M were used for k_D as well. 270 271 The bounds for r_A and d_A were determined based on detailed tiller demography measurements of *E. vaginatum* from Fetcher and Shaver (1983). The lower bounds for r_A and d_A ensure that the 272 proposed values yield initial tiller population growth and some proportion of tiller deaths. The 273 upper bounds for r_A and d_A use the maximum values observed across the range of sites and 274 experimental treatments in the study. They include disturbance and fertilization in order to 275 characterize the biological upper limit for the average of these parameters over the last ~ 250 276 years (see Figs. 1, 3, 4, and Table 4 in Fetcher and Shaver 1983). 277

278

The model parameterization utilized three observational data streams: tussock radius surveyed 279 across the North Slope, the relationship between tussock radius and tussock mass from our 280 harvest of tussocks, and the ratio between the number of live tillers and tussock radius from our 281 282 harvests. For each data stream, we calculated an individual cost function (i_i) as the total uncertainty-weighted squared data-model disagreement for each data type (Eqn. 10) which is a 283 284 function of the number of observations (N_i) for each data type (i), the data (y_i) , and the value predicted by the model at 250 years (p_i) (Richardson *et al.*, 2010). The standard deviation of all 285 286 the measurements was used as the uncertainty (δ_i) in the tussock radius and live tillers to radius ratio data streams. For the relationship between tussock radius and tussock mass, the uncertainty 287 288 term was based on the standard deviation of the paired tussock radius measurements (Richardson et al., 2012). Tussocks reach maturity within 250 years (Mark et al., 1985). Hence we 289 incorporated an additional constraint (Richardson et al., 2010) wherein simulations were rejected 290 291 if the tussock radius did not reach an asymptotic growth trajectory within that time.

$$j_i = \sum_{1}^{N_i} \left(\frac{y_i - p_i}{\delta_i}\right)^2$$
 Eqn. 10

293 In step one, parameters were proposed using a normal distribution with a mean equal to the 294 previously accepted parameter and a standard deviation equal to a fraction of the initial 295 parameter range. The standard deviation was adjusted to achieve an acceptance rate of 25 - 30%and to prevent the routine from getting stuck at local minima. Parameters that fell outside of their 296 297 data-informed prior range were re-drawn. The parameter space was explored for 50,000 iterations. The best parameter set was the one that minimized the overall cost function (J, Eqn. 298 299 11). This overall cost function treats all data streams equally and values relative improvements in goodness-of-fit (Franks et al., 1999; Richardson et al., 2010). 300

$$J = \prod_{i} j_i$$
 Eqn. 11

301

Step two estimated parameter uncertainty by exploring the parameter set that yielded the smallest 302 303 value for J in step one. Parameter values were drawn from a normal distribution with a mean equal to the best parameter set from step one and a standard deviation which was held constant at 304 305 the adjusted value from the end of step one. Uncertainty-weighted data-model disagreements were normalized based on the variance of the *j*'s obtained in step one. Parameter sets were 306 accepted if the cost function for each data stream (j_i) passed a chi-squared test (CI = 90%) 307 (Franks et al., 1999; Richardson et al., 2010; Keenan et al., 2012; Wright & Rocha, 2018). Step 308 309 two yielded 10,000 accepted parameter sets, chosen to balance the need to capture the 310 distribution of tussock sizes and the computational time.

311

We assessed parameter sensitivity by plotting LOESS smoothed predicted radius at 250 years for the parameter sets obtained in step two versus the parameters used in those predictions. The difference in LOESS smoothed predicted tussock radius at 250 years for the minimum and maximum parameter sets obtained in step two was used as a sensitivity measure. We also manipulated the constrained model by making predictions with tiller radius altered to extremely large (0.64 cm) and extremely small (0 cm) values to demonstrate the impact of different parameters and processes on the model predictions.

- 320 **3. Results**
- 321

322 *3.1 In-situ tussock development and size*

- 323 Tussock development and size were mostly dependent on disturbance history and tussock age 324 and less so on environmental conditions. At the disturbed Eagle creek bladed (EC-B) site with young tussocks, the average tussock radius significantly increased at a rate of 0.25 ± 0.06 cm y⁻¹ 325 (P<0.001; Fig. 3a). At the undisturbed sites with older tussocks (EC-U, CT-1, CT-2), the site 326 averaged tussock radius either remained unchanged or slightly declined (Fig. 3b). Across the 327 328 North Slope, the site averaged tussock radius was relatively constant and only weakly related to climate (Fig. S5; Table S1). Average growing season temperature only explained 15% of the 329 variation in site averaged tussock radius, while annual precipitation only explained 9% of the 330 variation in site averaged tussock radius. This relationship was weak despite a latitudinal decline 331 of 2.2 °C and 178 mm of precipitation across the measured sites. 332
- 333

334 *3.2 Tussock development and size model dynamics*

The impacts of hexagonal packing and limited carrying capacity for new tillers on tussock development were illustrated using the best fit parameter values for the model with modifications to tiller size (Fig. 4). Unrealistically small tillers minimized the impact of packing on tillering rate resulting in exponential tussock growth, while unrealistically large tillers enhanced the impact of tiller packing on tillering rate and resulted in tussocks that were unable to grow. Best fit tiller size fell in between these two extremes and resulted in tussocks that grew rapidly and approached steady-state size within 50 years (Fig. 4).

342

Temporal changes in tussock size were dependent upon the tussock's mass balance (Fig. 5a). Initially, tussock size increased when necromass gains exceeded necromass losses. Steady-state tussock size was reached when tussock mass gains equaled mass losses. This occurred when the packing index reached 1, indicating that there was insufficient space for new tillers, and tillering rates declined. Space limitation and declining tillering rates eventually stabilized the proportion of living and dead tillers atop the tussock (Fig. 5b).

349

350 *3.3 Model parameterization with model data fusion*

351 Model data fusion constrained the parameters of the tussock development model within the

ranges observed in the field. The posterior parameter distributions largely overlapped the

353 observed parameter distributions (Fig. 6). In some cases, the average for the posterior 354 distribution was slightly higher than for the observed distribution, especially for tiller radius and 355 the root input rate per tiller. This was likely due to measurement limitations or simplifications that were made to processes in the model. For example, the observed distribution for tiller radius 356 was informed by a mix of young and old tillers that differ in radius due to litter accumulation. 357 Consequently, the larger mean for the posterior tiller radius likely represents older accumulated 358 359 tillers rather than younger, recently developed tillers. Lastly, the posterior mean tiller root productivity was derived from peak biomass measurements and thus likely underestimates total 360 root productivity by not accounting for intraseasonal root turnover. 361

362

Model-data fusion constrained the posterior parameter distributions with reductions in the 363 interquartile range (IQR) and a shift towards roughly normal probability distributions (Table 1; 364 Fig. 6). The IQR for the dead tiller decomposition and removal rate decreased the most (25% of 365 prior IOR), whereas the IOR for the root input rate per tiller decreased the least (44% of prior 366 IQR). Five of the seven fitted parameters were strongly identifiable and weakly correlated during 367 368 the model data fusion (Fig. S6; Table S2). The two remaining parameters, the root necromass decomposition rate and the dead tiller decomposition and removal rate, were positively 369 370 correlated and, therefore more difficult to constrain independently. Nonetheless, the model-data fusion constrained their IQRs and yielded distributions that closely overlapped those observed in 371 372 the field (Fig. 6).

373

374 The model data fusion fitted parameters were able to replicate the observed distribution of steady-state tussock size, as well as the allometric relationships with steady-state live tiller 375 376 population and necromass. The model predictions of tussock radius replicated those observed across the North Slope, with the predicted distribution overlapping 95% of the observed 377 378 distribution (Fig. 7a). Modeled steady-state tussock radius ranged from 0.2 to 14 cm with a mean of 6 cm, while observed tussock radius ranged from 0.05 to 30 cm with a mean of 7 cm. 379 380 Tussocks at the high and low end of the distributions were less represented by the model. The 381 model captured the non-linear allometric relationship between steady-state root necromass and tussock radius, with the measured and modeled uncertainties overlapping for 86% of the 382 observations (Fig. 7b). The model also captured the non-linear allometric relationship between 383

steady-state living tillers and tussock radius, with the measured and modeled uncertaintiesoverlapping for 97% of the observations (Fig. 7c).

386

387 *3.4 Steady state tussock size sensitivity analyses*

Sensitivity analysis of the constrained model quantified the importance of each model parameter 388 in determining steady-state tussock size (Fig. 8). Physical parameters had the highest average 389 390 sensitivity, and demographic parameters had the lowest average sensitivity. In order from strongest to weakest sensitivity for physical factors, the root input rate per tiller was positively 391 related to tussock radius, and the root necromass decomposition rate and the dead tiller 392 decomposition and removal rate were negatively related to tussock radius. For structural factors, 393 root necromass bulk density and tiller radius were both negatively related to tussock radius. For 394 demographic factors, the per-capita tillering rate, the initial per-capita death rate, and the initial 395 per-capita population growth rate were all negatively related to tussock radius. The highest 396 overall sensitivity was associated with the root input rate per tiller with an 8.2 cm change in 397 predicted steady-state tussock size across the constrained parameter distribution. The second 398 highest overall sensitivity was associated with root necromass bulk density with a 6.6 cm change 399 in predicted steady-state tussock size across the constrained parameter distribution. 400

401

402 *3.5 Insights into steady-state tussock size*

The model sensitivity analyses provided hypotheses on the factors determining steady-state 403 tussock size that were independently tested with observations. We corroborated the predicted 404 405 sensitivity of steady-state tussock size to the most important measurable parameter in each category with observations. The independent field observations in Fig. 9 mirrored the model 406 407 sensitivity predictions in Fig. 8. Field observed tiller root productivity was positively related to tussock radius ($y = 3.5 \pm 1.0 + 79x \pm 14$, P < 0.001, R² = 0.5; Fig. 9a), while field observed root 408 necromass bulk density was negatively related to tussock radius ($y = 11.1 \pm 1.4 - 18.8x \pm 7.2$, P = 409 0.014, $R^2 = 0.17$; Fig. 9b). Field observed tillering rates exhibited a weak negative relationship 410 with tussock radius ($y = 10.41 \pm 1.6 - 9.02x \pm 5.18$; P = 0.09, R² = 0.08; Fig. 9c). The relative 411 importance of these factors in controlling tussock size mirrored that of the model sensitivity 412 analysis, as indicated by their R^2 and slopes. The observed relationship between tiller root 413 productivity and tussock size had the highest R^2 and slope, whereas tillering and tussock size had 414

415 the lowest R^2 and slope. The parallels between the constrained model sensitivities and the field

416 observations were surprising, given that the model was only constrained using the tussock size

distribution, the tussock live tiller allometry, and the necromass allometry. These parallels

418 provide further validation of the model's predictive ability since they emerged independently

419 from the mathematical representation of tussock development.

420

421 4. Discussion

422

Insights into the controls on tussock size were possible through model-data fusion and sensitivity 423 analysis of the constrained model. Model data fusion provided biological constraints for realistic 424 predictions of tussock size (Table 1; Figs. 6, 7). These constraints were necessary for the model 425 to reflect field observations of rapid growth in young tussocks and growth declines in mature 426 tussocks (Fig. 3). For example, the model demonstrated that tussocks grew exponentially without 427 the assumption of hexagonal packing and density-dependent tillering (Fig. 4). Synthesis of model 428 dynamics and observations indicated that site-averaged tussock size was attributed to intrinsic 429 physical and structural controls rather than extrinsic environmental controls (Figs. 3, 4, 5, 8). 430 These intrinsic controls manifested through feedbacks between tussock necromass balance, 431 432 available carrying capacity for new tillers, and density-dependent tillering (Figs. 4, 5, 8). The model sensitivity analyses also illustrated the importance of these feedbacks and provided 433 434 hypotheses about the main controls of tussock size that were independently validated with field data (Figs. 8, 9). 435

436

437 *4.1 What controls steady-state tussock size?*

438 Sensitivity analyses of the constrained model demonstrated that steady-state tussock size was largely controlled by both physical and structural factors and less so by demographic factors. 439 440 This makes intuitive sense, given the feedback between tussock necromass balance, available carrying capacity, and density-dependent tillering. The model explicitly linked the carrying 441 442 capacity (KA) to the amount of unoccupied space on top of the tussock through hexagonal tiller packing. Tussock growth only occurred when its mass balance was positive, resulting in 443 increased carrying capacity for new tillers and greater tiller root productivity to offset increasing 444 decomposition losses from the larger necromass pool. As tussocks aged, the population of dead 445

tillers increased, the total proportion of living tillers decreased, and cumulative decomposition 446 increased due to the increased size of the necromass pool. As a result, greater tiller root 447 448 production was needed to compensate for increasing decomposition losses in larger tussocks for tussocks to maintain a positive mass balance. The model also points to an important structural 449 property where a positive mass balance can be maintained longer and a larger tussock can be 450 achieved by reducing the structural requirement for the necromass pool through decreases in 451 452 bulk density. This process is consistent with the idea that the tussock mound microenvironment sustains the population of tillers atop the tussock (Chapin et al., 1979; Doust, 1981; Crain & 453 Bertness, 2005; Oliva et al., 2005; Lawrence & Zedler, 2011). It is also consistent with the 454 complex observed patterns of tiller population density, tussock radius, and tillering rates in E. 455 vaginatum tussocks, including a shift from high tillering rates in younger, smaller, less densely 456 packed tussocks to lower tillering rates in older, more densely packed tussocks (Fetcher & 457 Shaver, 1982; Fetcher & Shaver, 1983; Fetcher, 1985). The role of these processes in controlling 458 tussock development is further supported by the corroboration of the tussock size model 459 parameter sensitivities with observations (Figs. 8, 9). This strong agreement indicates that the 460 461 tussock model provided accurate insight into the controls on tussock development and size. 462

463 *4.2 Could latent factors provide alternate explanations for tussock size controls?*

Latent factors are those factors that were excluded from the mathematical model but may be 464 465 important for tussock growth and size. Soil anoxia, nutrient limitation, or biochemical signaling due to shading are three possible latent factors. Tussock necromass has a high moisture-holding 466 467 capacity that can induce anoxic conditions and decrease tiller root productivity in large tussocks (Stuart & Miller, 1982; Stuart & Miller, 1982; Gebauer et al., 1996). However, both field 468 469 observations and model sensitivity analyses exhibited the opposite response, with the highest root productivities being associated with large tussocks. Hence, soil anoxia is an unlikely latent 470 471 factor that explains tussock size constraints. Nutrient limitation also could constrain tussock size through 1) reduced tiller root input, 2) increased tiller death rates, or 3) reduced tillering rates 472 473 (Chapin et al., 1979; Shaver et al., 1986; Chapin et al., 1988). Factor 1 was deemed unimportant given that large old tussocks had the highest tiller root productivity (Figs. 8,9), and factor 2 was 474 also deemed unimportant given the weak negative relationship between the initial per-capita 475 476 death rate and tussock size indicated by the model sensitivity analyses (Fig. 8). Reduced tillering 477 rates can occur for both nutrient limitation and shading scenarios. (Fetcher & Shaver, 1982; 478 Fetcher & Shaver, 1983; Fetcher, 1985). Increased nutrient limitation with tussock size may limit 479 tillering rates through decreased resources, while increased shading reduces the red:far-red ratio. Changes in red:far-red ratio likely affect the ratio of active to inactive forms of phytochrome and 480 decrease tillering rates in large old tussocks with densely packed tillers (Deregibus *et al.*, 1983; 481 Deregibus et al., 1985; Fetcher, 1985; de Kroon & Kwant, 1991; de Kroon, 1993). Both of these 482 483 processes are incorporated indirectly into the model through density-dependent tillering rates and hexagonal packing. Therefore, we cannot rule out the role of nutrient limitation or shading on 484 decreased tillering rates but argue that the model may be capturing these dynamics without their 485 486 explicit representation in the model.

487

488 4.3. Implications for representing tussocks and their response to climate change in TBMs Our analyses elucidate the unique and important role of belowground processes in regulating 489 490 tussock size and tussock necromass C stocks. Many of these processes are not represented in 491 current TBMs (Epstein et al., 2001; Dorrepaal, 2007; Sullivan et al., 2007; Wullschleger et al., 2014; Iversen et al., 2015; Mekonnen et al., 2021). For example, TBMs currently represent 492 tussocks using non-tussock forming sedge or C3 grass PFTs (Wullschleger et al., 2014; McGuire 493 494 et al., 2018; Mekonnen et al., 2021; Curasi et al., 2022). These PFTs do not explicitly represent tussock necromass or the important feedbacks between aboveground and belowground processes 495 496 that determine tussock size as presented here. Such interactions are important since tussocks can have direct and indirect impacts on arctic C cycling. For example, tussock size also impacts other 497 ecosystem properties that interact with C cycling, such as microtopography, soil temperature, 498 and nutrient cycling (Chapin et al., 1979; Gebauer et al., 1996; Gersony et al., 2018). 499 500 Consequently, we argue that incorporating tussock aboveground and belowground interactions and feedbacks into TBMs will provide a more realistic representation of future arctic C cycling 501 502 predictions (Curasi et al., 2022).

503

Incorporating tussock-forming processes into TBMs will be challenging as it will require scaling the individual-based model to the ecosystem (Kyker-Snowman *et al.*, 2022). Both the model and field observations indicate strong intrinsic controls on tussock size, with environmental controls 507 exhibiting limited explanatory power for the belowground processes and feedbacks that regulate 508 tussock size. The model indicates that any climate-induced change in tussock size will depend on 509 the necromass balance mediated by tiller root input and root necromass decomposition. On one hand, tussock size in southern populations may decrease or remain unchanged if warming-510 induced increases in root necromass decomposition outweigh the stimulation of root productivity 511 (Hobbie, 1996; DeMarco et al., 2014; Parker et al., 2018). On the other hand, tussock size may 512 increase in northern populations if warming-induced stimulation of root productivity outweighs 513 increases in root necromass decomposition (Shaver et al., 1986; Lawrence & Zedler, 2011; Ma et 514 al., 2022). These expectations are somewhat supported by our observations. Smaller site 515 averaged tussock sizes were observed in cold far north sites, and tussock size remained 516 517 unchanged or decreased at more southern sites since the 1970s (Figs. 3, S5). Finally, scaling the individual-based model to the ecosystem will require an improved understanding of the 518 environmental controls on tussock density (i.e., the number of tussocks per unit area), as the 519 addition of a single tussock per unit area enhances soil organic layer C stocks by ~7% (Curasi et 520 al. 2022). 521

522

523 *4.4 Conclusion*

524 We presented a case study that integrated models and data to develop mechanistic insights into the complex long-term controls on an important foundation species in rapidly changing Arctic 525 526 ecosystems. These insights include the importance of belowground C allocation in regulating 527 tussock size and the intrinsic physical and structural controls on tussock C accumulation. The 528 results imply that future climate change is unlikely to affect the intrinsic controls on E. vaginatum tussock size, so future work should focus on better understanding belowground 529 processes within *E. vaginatum* and the factors regulating tussock abundance across the arctic. 530 The model could inform the representation of tussocks and their necromass C pool in TBMs 531 allowing tussock-forming processes to be included in ecosystems where they are present. This is 532 particularly relevant to the Arctic, where tussocks will influence the ecosystem's response to 533 climate change (Curasi et al., 2022). The tussock model also provides an opportunity to 534 determine whether the mechanisms regulating tussock size are similar across other tussock-535 forming grass and sedge species, given the large variation in tussock size that occurs across 536

grasses and sedges. These insights will facilitate a better understanding of the current and futurerole of tussocks in regulating ecosystem structure and function.

539

540 Acknowledgments:

- 541 Thanks to G. Shaver for your helpful comments and R. An, B. Blakely, D. Dech, C. Hammack,
- 542 N. Ho, I. Klupar, H. Long, M. Melendez, E. Niklinska, S. Unger, C. Vizza, M. Williams, and N.
- 543 Zimov, for their assistance. This work was supported by the National Science Foundation (DEB
- 544 1556772 to A.V.R., DGE 1841556 to S.R.C., PLR 1418010 to N.F.), the University of Notre
- 545 Dame, Fulbright (open study/research grant to S.R.C.), and National Geographic (Young
- 546 explorer grant to S.R.C). We also thank the Toolik field station, the Arctic LTER (NSF/PLR
- 547 1637459), the North East Science Station, and BP Exploration Alaska.

548

549 Author contributions:

- 550 S.R.C. and A.V.R. conceived the research. S.R.C, N.F., D. P. W., and A.V. R. collected the field
- data. S.R.C, K. S. W., and A. V. R. designed and conducted the modeling analysis. All authors
- 552 contributed to data interpretation and preparation of the manuscript text.

553

554 Data Availability:

- 555 The data and code which support this study are archived on Zenodo at
- 556 https://doi.org/10.5281/zenodo.6896732.

558 Figures:









Fig. 2: A conceptual diagram of our tussock growth model. Boxes represent state variables, solid
lines represent flows of material, circles represent derived quantities, dotted lines represent the

calculation of a derived quantity, and dashed lines represent constraints.



566 Fig. 3: Temporal dynamics in site averaged tussock radius at a) the disturbed Eagle creek bladed

site with young tussocks (EC-B) and at **b**) the Cape Thompson 1 and 2 (CT-1/2) and Eagle creek

undisturbed (EC-U) sites with old tussocks. Bars represent standard deviations.



569

570 Fig. 4: Temporal dynamics of tussock growth as influenced by extremely small- (hatched line),

571 medium-(solid line), and extremely large- (dotted line) sized tillers.



Fig. 5: Temporal dynamics of a) the components of necromass balance and packing index, and
b) the proportional of the total population composed of living (solid line) and dead (hatched line)
tillers atop the tussock using the best-fit parameters. In the a panel tussock mass inputs are
represented by a hatched line, mass outputs are represented by a solid line, and the packing index
is represented by a dotted line. The shaded gray area denotes a positive tussock mass balance and
associated tussock growth.



Fig. 6: The uniform prior bounds (dashed blue lines), the field data (black lines and black
histogram) from which the bounds were derived, and the constrained posterior probability
distributions (red lines) for the tussock size model parameters fitted with model data fusion.



584

Fig. 7: a) The steady state tussock radius probability distribution compared to the radius

- distribution from transect surveys (n = 2321). **b**) The relationship between root necromass and
- tussock radius at steady state compared to observations from harvested tussocks (n = 35). c) The
- relationship between the number of living tillers and tussock radius at steady state compared to
- observations from harvested tussocks (n = 35). The shaded red region in panels b and c
- represented the 90% confidence interval for model predictions.



Fig. 8: Steady-state tussock radius's sensitivity to the model parameters with 95% confidence
intervals. The parameter sensitivity, as shown in the upper right corner, is quantified as the
difference in average tussock radius after 250 years between the lowest and highest value in the
parameter distribution.



Fig. 9: Observed relationships between a) tiller root productivity, b) root necromass bulk
density, and c) offspring per adult tiller observed in harvested tussocks (n = 35) versus tussock
radius. Statistically significant relationships at the 95% confidence level are denoted with a
hatched regression line.

601 Tables:

Table 1: Description of state variables, free parameters, and other derived values. Prior ranges

- best fit model parameters and the percentage of the prior interquartile range are included for free
- 604 parameters.

Name	Symbol	Units	Prior (min, max)	Best fit	% of prior IQR			
	State	variables						
Live tillers	N _A	number of	-	-	-			
		tillers						
Dead tillers	N _D	number of	-	-	-			
		tillers						
Root necromass	M	g	-	-	-			
Free parameters								
Root necromass bulk density	ρ	g cm ⁻³	0.05, 0.26 ¹	0.11	39%			
Tiller radius	θ	cm	0.1, 0.25 ¹	0.21	32%			
Root input rate per tiller	α	g tiller ⁻¹ yr ⁻¹	0.003, 0.19 ¹	0.11	44%			
Root necromass decomposition rate	k _M	yr ⁻¹	0.006, 0.32 ¹	0.07	31%			
Initial per-capita population growth rate	r _A	yr ⁻¹	0.001, 0.5 ²	0.28	43%			
Initial per-capita death rate	d _A	yr ⁻¹	0.001, 0.5 ²	0.48	27%			
Dead tiller decomposition and removal rate	k _D	yr ⁻¹	0.006, 0.32 ¹	0.08	25%			
Other								
Carying capacity for live tillers	KΔ	number of	-	-	-			
	4	tillers						
Tussock radius	r	cm	-	-	-			
Tussock volume	V	cm ³	-	-	-			
Per-capita tillering rate	b	yr⁻¹	-	-	-			

606 See ¹2.3 Tussock allometry, tiller characteristics, and decomposition, ²Fetcher and Shaver

607 (1983).

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611.

- **Fig. S1** Map of the survey sites and the historical survey sites.
- **Fig. S2** Relationships between tussock radius, root necromass, and tussock height.
- **Fig. S3** The relationship between tussock radius and the total number of tillers atop a tussock.
- **Fig. S4** Graphical representation of the population model parameters.
- **Fig. S5** Boxplot of surveyed tussock radius and climate.
- **Fig. S6** Parameter correlation plots.
- 828 **Table S1** R2 and P values for the correlation analysis.
- 829 **Table S2** Pearson correlation coefficients for data assimilation.

830 Methods S1 Algebraic manipulation of Equation 4.