Integrating Arctic plant functional types in a land surface model using above- and belowground field observations

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Abstract

Accurate simulations of high latitude ecosystems are critical for confident Earth system model (ESM) projections of carbon cycle feedbacks to global climate change. Land surface model components of ESMs, including the E3SM Land Model (ELM), simulate vegetation growth and ecosystem responses to changing climate and atmospheric CO2 concentrations by grouping heterogeneous vegetation into like sets of plant functional types (PFTs). Such models often represent high-latitude vegetation using only two PFTs (shrub and grass), thereby missing the diversity of vegetation growth forms and functional traits in the Arctic. Here, we use field observations of biomass and leaf traits across a gradient of plant communities on the Seward Peninsula in northwest Alaska to replace the original ELM configuration for the first time with nine arctic-specific PFTs. The PFTs that are new to the model include: 1) nonvascular mosses and lichens, 2) deciduous and evergreen shrubs of various height classes, including an alder PFT, 3) graminoids, and 4) forbs. Improvements relative to the original model configuration included greater belowground biomass allocation, persistent fine roots and rhizomes of nonwoody plants, and better representation of variability in total plant biomass across sites with varying plant communities and depth to bedrock. Simulations through 2100 using the RCP8.5 climate scenario showed alder-dominated plant communities gaining more biomass and lichen-dominated communities gaining less biomass compared to default PFTs. Our results highlight how representing the diversity of arctic vegetation and confronting models with measurements from varied plant communities improves the representation of arctic vegetation in terrestrial ecosystem models.

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14 15 16 17 18 19 20	 Key points Biomass measurements of arctic plants in the Seward Peninsula were used to develop nine arctic plant functional types in the E3SM Land Model New plant functional types included mosses, lichens, graminoids, and shrubs of different height classes and leaf habits Simulations across a gradient of plant communities showed how variations in plant traits and soil depth drive different biomass patterns
21 22 23	Abstract

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26 components of ESMs, including the E3SM Land Model (ELM), simulate vegetation growth and

- ecosystem responses to changing climate and atmospheric CO_2 concentrations by grouping heterogeneous vegetation into like sets of plant functional types (PFTs). Such models often
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- 34 and lichens, 2) deciduous and evergreen shrubs of various height classes, including an alder PFT,
- 35 3) graminoids, and 4) forbs. Improvements relative to the original model configuration included
- 36 greater belowground biomass allocation, persistent fine roots and rhizomes of nonwoody plants,
- 37 and better representation of variability in total plant biomass across sites with varying plant
- 38 communities and depth to bedrock. Simulations through 2100 using the RCP8.5 climate scenario 39
- showed alder-dominated plant communities gaining more biomass and lichen-dominated 40 communities gaining less biomass compared to default PFTs. Our results highlight how
- 41 representing the diversity of arctic vegetation and confronting models with measurements from
- 42 varied plant communities improves the representation of arctic vegetation in terrestrial
- 43 ecosystem models.
- 44

45 **Plain language summary:**

46 Arctic ecosystems are home to specialized plant communities that have adapted to cold winters

- and short growing seasons. Arctic plant communities include a diverse group of plants with 47
- 48 different heights and growth patterns, and these different types of plants are likely to respond
- 49 differently to a warming climate and rising atmospheric carbon dioxide concentrations.
- 50 However, the computer models that are used to predict how ecosystems and climate will change
- 51 in the future include only a small number of Arctic plants. We used measurements of plant
- 52 biomass across different plant communities in the Seward Peninsula of Alaska, USA to add new
- 53 types of arctic plants to an ecosystem model. We then simulated how ecosystems would respond
- 54 to a warming climate and rising levels of atmospheric carbon dioxide using both original and
- 55 updated versions of arctic plants in the model. The new plant types allowed the model to
- 56 simulate how ecosystems dominated by tall shrubs could gain biomass at much faster rates than 57
- ecosystems with thin soils and small plants. Our results show how including the diversity of
- 58 arctic plants can improve model predictions of vegetation responses to climate change in the 59 Arctic.

Introduction: 1 60

The Arctic region is warming twice as fast as the global average (Hartmann et al., 2013), 61 driving substantial changes in both soil and vegetation dynamics in the region (Myers-Smith et 62 63 al., 2019; Schuur et al., 2015; Turetsky et al., 2020). Earth system models, such as the Energy Exascale Earth System Model (E3SM; Golaz et al., 2019) rely on simulations of terrestrial 64 65 ecosystems to provide the lower boundary conditions of the atmosphere and to simulate the 66 terrestrial cycling of carbon (C), nutrients, water, and energy. Land surface models, including the 67 E3SM Land Model (ELM) (Yang et al., 2019), simulate vegetation growth and mortality along 68 with soil processes such as organic matter decomposition and hydrology. Permafrost soils in the 69 Arctic hold an estimated 1300 Pg of organic C when integrated to 3-m depth (Hugelius et al., 70 2014). Thus, biogeochemical cycling in this region is critical to global climate simulations due to 71 the potential for C cycle feedbacks to climate change, including increasing C emissions to the 72 atmosphere due to decomposition of thawing permafrost (Koven et al., 2011; Schuur et al., 2015) 73 or, conversely, increased arctic plant C uptake related to lengthening growing seasons, 74 expanding shrub areas, or increasing nitrogen (N) availability (Myers-Smith et al., 2015; Qian et 75 al., 2010; Salmon et al., 2016; Shaver et al., 1992).

76 Changes in the distribution of vegetation across the landscape, as well as in the 77 composition and associated traits of tundra plant communities, also drive biophysical feedbacks 78 to climate, including changes in albedo associated with shifting plant communities (Sturm et al., 79 2005) and changing transpiration rates associated with changes in leaf area and woody 80 vegetation ranges (Pearson et al., 2013), as well as complex interactions among vegetation and 81 soil temperature (Loranty et al., 2018). For example, vegetation height is a key factor in Arctic 82 biophysical climate feedbacks. While trees and tall shrubs can extend above snow, decreasing 83 winter albedo (Loranty et al., 2014) or driving earlier snowmelt (Wilcox et al., 2019), patches of 84 taller vegetation can also trap snow, insulating the ground and keeping soils warmer during 85 winter (Sturm et al., 2001). In turn, shading of the ground can exert a cooling effect during the 86 warmer, snow-free season (Myers-Smith & Hik, 2013).

87 The Arctic is home to specialized low-stature tundra plant communities adapted to 88 environmental and climatic extremes, with typically low summer temperatures and a short 89 growing season. The region supports plants such as dwarf shrubs, forbs, lichens and mosses that 90 all grow close to the ground. The amount of warmth available for plant growth increases as one 91 moves south from the high Arctic, and the stature, abundance, and diversity of plants tends to 92 increase as well. The distribution of plant communities is primarily controlled by landscape, 93 topography, soil chemistry, soil moisture, and the plants that historically colonized an area 94 (Raynolds et al., 2019; Thomas et al., 2020). In addition, plant communities also vary in their 95 composition of plant functional types (PFTs), or groupings of plant species that share similar 96 growth forms and roles in ecosystem function (Wullschleger et al., 2014).

97 In topographically and hydrologically diverse landscapes like the central Seward 98 Peninsula of Alaska in the low Arctic, plant communities comprise a variety of graminoid, shrub, 99 and lichen-dominated community types (Raynolds et al., 2019). In addition to canopy heights 100 driving biophysical feedbacks, the varying growth patterns, biomass allocation patterns, and life 101 history strategies of arctic PFTs result in an array of survival patterns and potential responses to 102 warming (Bjorkman et al., 2018). Distributions of different arctic PFTs and traits are already 103 changing under warming conditions (Epstein et al., 2012; Myers-Smith et al., 2011, 2015; Tape 104 et al., 2006). As a result, accurate representation of the diversity of PFTs in arctic ecosystems, 105 and of their specialized physiologies, is necessary to produce reliable model projections of arctic 106 ecosystem responses to warming and other climatic changes (Rogers et al., 2017).

107 Arctic PFT classifications include evergreen and deciduous shrubs, forbs, graminoids 108 (grasses, sedges, rushes), lichens, and bryophytes (mosses and liverworts) (Figure 2; Breen et al., 109 2020). These PFTs have been further differentiated by various factors such as by plant stature 110 (dwarf, low, tall; Walker et al., 2005) or species (Sphagnum moss, Non-Sphagnum moss; Chapin et al. 1996). Key Arctic vegetation traits such as stature, leaf area, and leaf N are not well 111 112 differentiated by the few and coarse functional groups typically used in land surface models 113 (e.g., deciduous shrub, evergreen shrub, graminoid, and forb) (Thomas et al., 2019; Wullschleger 114 et al., 2014). For example, a ubiquitous deciduous dwarf shrub such as Salix arctica, that is 115 prostrate rather than erect, has a maximum height of a few centimeters and will not grow taller 116 even under ideal environmental conditions. In contrast, low to tall erect shrubs may vary in 117 height depending on habitat and growing season temperature. In one study, the deciduous low to 118 tall shrub Salix richardsonii was shown to vary in maximum mean height across a latitudinal 119 transect from approximately 10 cm in open tundra on the Alaskan arctic coast where mean July 120 temperature was 2.6 °C to >200 cm at streamside sites in the base of the foothills of the Brooks Range where mean July temperature was 10 °C (D. A. Walker, 1987). Thus, changes in plant 121

122 biomass and height are constrained by the exact species or PFT present in a plant community.

- 123 However, the current configuration of ELM, similar to other global land surface models such as
- the Community Land Model (CLM5; Lawrence et al., 2019), represents Arctic vegetation using
- only a small number of plant functional types (PFTs) (Wullschleger et al., 2014). In the default
 configuration of ELM used in global simulations (largely inherited from CLM4.5), arctic PFTs
- are divided into one broadleaf deciduous boreal shrub and one C3 arctic grass (Oleson et al.,
- 2013). This structure limits the ability of the model to represent the diversity of growth forms in
- 129 Arctic ecosystems as well as their associated responses to warming (Epstein et al., 2001). For
- 130 example, the single boreal deciduous shrub PFT in ELM cannot represent the contrast in
- 131 potential warming responses and biomass distributions of ecosystems dominated by shrub PFTs
- 132 that differ in their stature and potential height. Because an increase in vegetation height in a
- dwarf-shrub dominated plant community often means a change in species composition
- 134 (Bjorkman et al., 2018), a model lacking such trait variations among species might predict an
- inaccurate growth response to warming. Representation of vegetation trait variation has been shown to affect C avaling at global scales, making it a priority for improving the accuracy of
- shown to affect C cycling at global scales, making it a priority for improving the accuracy ofESMs (Verheijen et al., 2015).
- In addition to missing variability in aboveground vegetation traits such as stature, models with few Arctic PFTs, such as ELM, also poorly represent above- and belowground partitioning of growth and biomass as observed in Arctic vegetation (Chapin et al., 1996; Song et al., 2017). In particular, Arctic shrubs and graminoids allocate a large fraction of their growth to belowground root and rhizome tissues that persist over multiple growing seasons (Iversen et al.,
- 142 2015). A comparatively smaller fraction of growth is expressed in leaves and other aboveground
- 144 tissues, which can persist for multiple seasons even in graminoids, reflecting the short growing
- season and resulting need for conservative growth strategies (Jonasson & Chapin, 1985; Shaver
- 146 & Laundre, 1997). ELM, however, represents graminoids as deciduous plants that allow both
- 147 leaves and fine roots to senesce every year. Graminoids in ELM only have leaf, fine-root, and 148 nonstructural storage biomass pools, with no representation of rhizomes or other tissues that last
- more than a year, but which can be key to longevity and survival in environments with short
- growing seasons and cold winters (Van Groenendael et al., 1996) as well as providing the basis
 for lateral growth (Klimešová et al., 2018). Finally, ELM does not include specific representation
- 152 of bryophyte or lichen growth or biomass. Many Arctic ecosystems are dominated by such
- 153 cryptogam biomass (D. A. Walker et al., 2016), with important implications for carbon storage 154 and responses to fire and grazing pressure (Joly et al., 2009; Longton, 1997). Bryophytes and
- 155 lichens also have different albedo and other surface properties and do not transpire in the same
- 156 way as vascular plants, making them important for accurately representing biophysical and
 157 hydrological interactions with the atmosphere in land surface models (Druel et al., 2019; Porada
- 158 et al., 2016; Stoy et al., 2012).
- 159 As part of the Next Generation Ecosystem Experiment (NGEE) Arctic project, field sites 160 were established on the Seward Peninsula of Alaska and plant composition, traits, and biomass 161 allocation were characterized across hillslope and hydrological gradients, with the goal of evaluating and improving predictive capabilities of models in arctic ecosystems (Breen et al., 162 2020; Iversen et al., 2019b, 2019a; Salmon et al., 2019d, 2019c, 2019b data citations). For the 163 purposes of this analysis, we used observations from six dominant plant communities spanning 164 the Kougarok Hillslope field site located on the Seward Peninsula, AK (65°09'50.1"N, 165 166 164°49'34.2"W; see Figure 1) to parameterize Arctic-specific PFTs within ELM. We then used
- 167 those PFTs in different assemblages and relative cover fractions to simulate the distinct plant

- 168 communities within ELM. We applied versions of ELM with configurations ranging from site-
- specific plant traits and community assemblies to a global-scale model grid cell to address two
- 170 research questions: (1) What is the relative importance of root-available soil depth, tundra plant
- species traits, and tundra plant community composition for improving model simulations of
- 172 vegetation biomass and its variability across a landscape of low Arctic tundra plant
- 173 communities? (2) How does the incorporation of measurement-constrained, tundra-specific plant
- 174 functional types and soil depths affect projected vegetation biomass responses to increasing
- 175 temperatures and atmospheric CO_2 concentrations over the 21^{st} century?

176 2 Methods:



177 2.1 Site and measurements

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179

- Figure 1: Location of Kougarok Hillslope field sites on the Seward Peninsula of Alaska, USA, at
 mile marker 64 on the Kougarok road north of Nome, Alaska (Iversen et al., 2017; data citation).
 Panel (c) shows visual imagery, elevation (m), and individual plot locations colored according
- 183 to community type. See Table 1 for full community type names and definitions.
- 184

Vegetation data were collected at the peak of the growing season in mid to late July 2016 and 2017 at the NGEE Arctic Kougarok Hillslope field site located in the interior of the Seward Peninsula of Alaska (65°09'50.1"N, 164°49'34.2"W; Figure 1). The hillslope is comprised of an exposed, rocky outcrop with alpine vegetation at its summit surrounded by steep, well-drained slopes that transition to gently sloping alder savanna in water tracks and graminoid tussock-

- 190 lichen tundra in inter-water tracks, and then to lowland wet tundra. The hillslope spans a roughly
- 191 100 m change in elevation and a variety of plant communities are present across the varying
- 192 topography (Figure 2). Alder shrublands are found along the well-drained slopes below the crest
- 193 of the hill and are interspersed with patches of willow-birch and dwarf shrub lichen tundra.
- 194 Extensive field site details are described in Salmon et al. (2019a).
- 195 We surveyed the six dominant plant communities along the hillslope, which varied in 196 their shrub abundance, canopy height, and structure, to characterize the vegetation composition 197 at the site following the recommended protocol of Walker et al. (2016) (Breen et al., 2020; data 198 citation) (Table 1, Figs. 2, 3). Five replicate vegetation composition plots from each plant 199 community were chosen subjectively in areas of homogeneous and representative vegetation and varied in size from 1-25 m² depending on canopy structure and height. The surveyed plot area 200 201 was 1 x 1 m for all plant communities except for the taller stature willow-birch tundra (2.5 x 2.5 202 m) and alder shrubland (5 x 5 m). For each plot, all plant species (vascular plants, lichens, and 203 bryophytes) were recorded along with visual estimates of their percent cover. For plots with 204 multiple canopies, field cover estimates are absolute cover, meaning that the total cover per plot 205 can be >100%. We calculated relative cover values (adding to 100%) from the field data and use 206 these for all subsequent analyses. Plant species were further aggregated into nine PFTs based on growth patterns and plant traits (see Breen et al., 2020 dataset for a full species list with PFT 207 208 designations). Biomass sampling plots were paired with a subset of vegetation composition plots 209 distributed across the six dominant plant communities (Table 1), with two replicate plots per
- community.



- 211
- 212 Figure 2: Toposequence figure of the Kougarok hillslope showing the distribution of plant
- 213 functional types and communities along with underlying soil layers. Vegetation and soil depths
- not drawn to scale. PFTs are listed that within each hillslope and the dominant PFTs (mean
- cover >15%) are indicated in bold. See Table 1 for full names and definitions of plant
- 216 *communities*.



Figure 3: Representative photographs of the six plant communities. See Table 1 for full names and definitions.

217

218 For all deciduous low to tall individuals in the plots (*Alnus viridis* ssp. *fruticosa*, *Betula*

glandulosa, *Salix alaxensis*, *S. glauca*, *S. pulchra*, and *S. richardsonii*) maximum shrub height
and stem basal diameters were measured. We then performed a destructive harvest of one

individual for each of the low-to-tall shrub species present in the plot to determine whether
existing allometries could be applied. Following the destructive harvest of these low-to-tall shrub
species, we separated attached dead leaves, inflorescences, live leaves, attached dead wood, live
wood, and current year's stem growth. The dry aboveground biomass of harvested shrubs was
within the range of published allometric relationships (see Supplementary Figure 1 and Berner et al., 2015). We consequently used Berner et al. (2015)'s allometric equations to determine
aboveground biomass and NPP for the low to tall shrubs we surveyed but did not harvest. The

- aboveground biomass and NPP for the low to tall shrubs we surveyed but did not harvest. The
 allometric relationships in Berner et al. (2015), however, do not separate leaf biomass from stem
- biomass. To quantify leaf biomass, we applied the ratio of leaves to the sum of new leaves and
- stems observed in our harvest. The ratios in our data (0.80-0.87) were similar to values observed
 within a subset of the Berner et al. (2015) data (0.80, *personal communication*). We assumed leaf
- NPP for deciduous shrubs was equivalent to the entire leaf pool. Stem NPP is the sum of primary
- stem NPP (extension of new stem) plus secondary stem NPP (thickening of existing stems).
- 234 Primary stem NPP was calculated as the NPP from Berner's allometric equations minus the leaf
- 235 NPP. Secondary stem NPP was calculated based on ratios of secondary stem growth to primary
- stem growth observed for *Salix* and *Betula* at the Toolik Field Station Arctic LTER Site (Bret-
- Harte et al., 2002). The ratio applied to *Alder* (henceforth 'alder shrubs') was an average of *Salix*and *Betula*.
- Above ground biomass of understory vegetation was sampled using $20 \text{ cm} \times 50 \text{ cm}$ clip plots (Salmon et al., 2019b). Understory species include bryophyte, lichen, graminoid, forb, and
- shrub PFTs (Table 1). All material from understory clip plots was cut at the level of the moss or
- soil surface and sorted by tissue type (stem versus leaf) and tissue age (current year versus
- 243 older). Live moss was distinguished from dead based on color and live liverworts were combined

with live mosses as part of the bryophyte PFT. Net primary productivity was calculated based on
new versus old tissues and leaf habit of the plant. Note that while deciduous dwarf shrubs were
observed in plant survey plots, none occurred in biomass sampling plots.

247 Fine-root biomass and rooting depth distribution were measured on n = 2 soil cores 248 collected within each of the biomass plots (n = 2 biomass plots per plant community) (Salmon et 249 al., 2019c). In the field, 7.62-cm diameter soil cores were taken to the depth of rock or frozen 250 soil and separated into depth intervals of roughly 10 cm. Soil depth was estimated using a thaw 251 depth probe, noting whether the resistive layer the probe encountered was rock or frozen soil. 252 Soil depth increments were frozen and shipped to ORNL for processing. In the lab, intact soil 253 depth increments were divided in subsections where one subsection was used to determine soil 254 properties and the other subsection was used to assess the biomass of living fine roots (<2 mm 255 diameter). Roots were classified as live based on tensile strength and morphology. Fine roots 256 could not be reliably attributed to specific species or PFTs, and fine-root biomass was therefore 257 aggregated at the plot level for analyses. Fine-root production was estimated using community-258 specific, average lifespan estimates of fine-root populations from similar Arctic plant 259 communities (Table S2).

260 Rhizome biomass and belowground stems were not directly measured because soil cores
261 were not large enough capture their spatial variability, and aboveground surveys could not
262 capture this belowground pool. Rhizome biomass was therefore estimated using relationships
263 between aboveground biomass and rhizomes for PFTs and plant communities observed at Toolik
264 Lake (Shaver & Chapin, 1991).

Leaf areas of understory clip plots and shrub harvests were measured by scanning entire leaves (WinRHIZO, Regent Instruments Inc., Quebec, Canada) or by taking leaf punches with a known diameter. Leaves and leaf punches were then dried and weighed so that leaf area and mass could be used to calculate Specific Leaf Area (SLA, cm^2/g). Leaf, stem, and fine roots from understory clip plots, shrub harvests, and soil cores were dried, ground, and analyzed for

- 270 %C and %N by weight on an elemental analyzer (Costech ECS 4010, Costech Analytical
- 271 Technologies, Inc., Valencia, CA, USA).

All measured plant biomass, NPP, and tissue characterization data were aggregated over species to the PFT level. Each plant community was thus defined as an assembly of PFTs with the relative cover of each PFT varying by plant community. These relative covers were then used to drive community-specific simulations in ELM (see below). 276

- 277 Table 1: Kougarok Hillslope dominant plant communities. Observed soil depth indicates the measured depth to a resistive layer
- 278 (Iversen et al., 2019a) and whether the resistive layer was rock or frozen soil. Note that in the model, soil depth to rock was assumed
- to be the level at which a thaw probe encountered primarily rocky material, or alternatively, the model maximum soil depth of 3.8 m if
- 280 the probe reached frozen soil rather than rock. Measured depth to frozen soil was not used to configure model soil depth because ELM
- simulates thaw depth dynamically (Section 2.2).

CAVM Physiognomic Map Unit Name (Raynolds et al. 2019)	Plant Community Name	Brief description	Max observed vegetation height (cm)	Observed soil depth (cm)		
Barrens and barren complexes: cover of vascular plants.	Areas with predo	minantly barren soils or bedrock, or covered by biologica	ll soil crusts but lac	king much		
Carbonate mountain complex; and more specifically prostrate dwarf-shrub, herb, lichen tundra at higher elevation	Dryas-lichen dwarf shrub tundra (DLST)	Dry tundra with patchy vegetation. Dominated at our site by <i>Dryas punctata</i> ssp. <i>alaskensis</i> (equivalent to <i>D. octopetala</i> ssp. <i>alaskensis</i>) and other prostrate dwarf shrubs with graminoids and forbs. Lichens are abundant. Occurs on the rocky, exposed outcrop at the summit and hillcrest.	23	10 (rock layer)		
Graminoid tundras: Areas with high latitudes and ice-rich permat	tundra vegetation frost areas in the le	dominated by graminoid plants (sedges, grasses and rush ow Arctic.	es), mainly in mes	ic areas at		
Tussock- sedge, dwarf-shrub, moss tundra	Tussock-lichen tundra (TT)	Moist tundra, dominated by tussock cottongrass (<i>Eriophorum vaginatum</i>) and dwarf shrubs. Mosses are abundant. Occurs along the backslope and footslope of the hill between water tracks.	38	33 (frozen layer)		
Erect-shrub tundras: Areas with tundra vegetation dominated by erect dwarf shrubs or low shrubs and mosses mainly in mesic areas.						
Erect dwarf-shrub, moss tundra	Birch- Ericaceous lichen shrub tundra (BEL)	Moist tundra dominated by erect dwarf shrubs (<i>Betula nana, Empetrum nigrum, Arctous alpina, Kalmia procumbens</i>) and abundant lichens. Occurs on the hillcrest and shoulder of the hill.	27	26 (rock layer)		

Low-shrub, moss tundra	Willow-birch tundra (WBT)	Moist acidic shrublands dominated by low to tall shrubs (<i>Salix</i> spp., <i>Betula nana, B. glandulosa</i>), dwarf shrubs and mosses. Occurs on the backslope of the hill.	146	32 (frozen layer)
	Alder savanna (ASV)	Moist tussock-lichen tundra with patches of alder (<i>Alnus viridis</i> ssp. <i>fruticosa</i> , < 2 m tall) and other low and dwarf shrubs. Occurs in water tracks on the lower backslope and footslope.	132	35 (frozen layer)
	Alder shrubland (AS)	Moist acidic shrublands on hillsides with closed low to tall alder (<i>Alnus viridis</i> ssp. <i>fruticosa</i>) canopies. Low and dwarf shrubs are also abundant. Occurs on the upper backslope in a band below the hillcrest and shoulder of the hill.	320	20 (rock layer)

282 2.2 Default land model description

283 The E3SM Land Model (ELM) is the land surface component of E3SM. ELM simulates 284 water, energy, C, N, and P cycles in terrestrial ecosystems. Here, we briefly describe model 285 processes relevant to this study. For additional model description, see (Burrows et al., 2020; 286 Ricciuto et al., 2018; Yang et al., 2019). ELMv1 branched from CLM4.5 (Oleson et al., 2013, 287 equivalent to ELMv0), and incorporates new developments including P cycling (Yang et al., 288 2019). C, N, and P cycles are simulated in vegetation and soil organic matter. Vegetation is 289 divided into multiple PFTs with independent parameterizations controlling photosynthesis, leaf 290 gas exchange, biomass allocation, and other processes. Biomass growth allocation among 291 different tissues is based on fixed allocation ratios relating leaf, fine-root, aboveground woody 292 tissue (stem), and belowground woody tissue (coarse-root) growth fractions. Woody tissues are 293 divided into living (e.g., respiring sapwood) and dead (e.g., non-respiring heartwood) fractions. 294 Plants are divided into tree, shrub, and non-woody types. Trees and shrubs both have woody 295 tissues but use different calculations for biomass allocation to woody tissue and different 296 allometric parameters for calculating canopy height. Non-woody PFTs in the default model are 297 assumed to have only leaves and fine roots. Each PFT also has nonstructural storage pools for C, 298 N, and P. Deciduous plants use these nonstructural pools to grow leaves and fine roots in the 299 spring, and to store C and nutrient uptake in nonstructural pools during the growing season for 300 use in the next season. The fraction of nonstructural C and nutrient pools used each spring season 301 by deciduous plants is set to 50% in the default model configuration. Evergreen plants in the 302 unmodified model grow biomass throughout the growing season in connection with current 303 photosynthesis, with nonstructural pools used only under nutrient-limited conditions. 304 Maintenance respiration of living tissues (including leaves, fine roots, and living woody tissue) is 305 a function of tissue N content and modified by a Q10 temperature dependence. Leaf respiration 306 is assumed to stop when plants are under snow, but root respiration does not include a dormancy 307 factor in the default ELMv1 model configuration. ELM simulates energy and water dynamics in 308 soil including liquid and frozen water content and dynamic active layer thickness.

309 2.3 Model changes

310 2.3.1 Soil depth to bedrock

ELM uses a default soil depth to bedrock of 3.8 m. Roots, water flow, and soil biogeochemistry 311 312 are only simulated in layers above the bedrock depth. In addition to the bedrock layer, ELM 313 simulates a dynamic active layer thickness (ALT) at sites underlain by permafrost as the deepest 314 thawed layer in the modeled soil temperature profile. Plant roots in the model are not permitted 315 to grow deeper than the maximum active layer thickness from the previous growing season. 316 Measured soil depth to rocky layers varied substantially across vegetation communities (Table 317 1). The DLST community in particular had very shallow soils and significant areas of exposed 318 rock. For this study, ELM was configured to use measured soil depth to the rocky layer as depth 319 to bedrock in plant communities with shallow rocky layers to test the importance of this abiotic 320 site factor in simulated biomass and NPP; for the purposes of this analysis, those communities 321 were DLST, BEL, and AS (Table 1). For model simulations, soil depth to rock was assumed to 322 be the level at which a thaw depth probe encountered primarily rocky material, or the model

maximum soil depth of 3.8 m if depth probes reached frozen soil rather than rock. Measured
 depth to frozen soil was not used to configure model soil depth because ELM simulates thaw
 depth dynamically. Model active layer thickness was not modified based on site measurements.

326 2.3.2 PFT changes

327 Default ELM PFTs are based on broad groups relevant for global-scale configurations 328 (Wullschleger et al., 2014). These include one broadleaf deciduous boreal shrub PFT and one C3 329 arctic grass PFT that was assumed to be annual, allowing leaves and fine roots to senesce at the 330 end of each growing season. No non-vascular PFTs (lichens or bryophytes) were included in the 331 default ELM PFTs. To match the observed plant diversity at the Kougarok Hillslope field site, 332 we defined new ELM PFTs based on literature and site measurements and altered model 333 functionality to match observed Arctic plant traits (Table 2). The original model's deciduous 334 broadleaf boreal shrub was divided into five different shrub types, representing the diversity of 335 leaf habits (both evergreen and deciduous types occur at the Kougarok Hillslope site) and 336 differences in growth patterns including potential maximum height and aboveground-337 belowground partitioning. Dwarf prostrate shrubs, such as Salix arctica, reach a maximum 338 height of 10 cm, while dwarf erect shrubs are <40 cm tall. Low shrubs vary from 40 cm to 2 m in 339 height. Low-to-tall shrubs can potentially reach over 2 m in warmer microsites depending on 340 growing conditions. Deciduous low to tall shrubs were further divided into alder and non-alder 341 (willow and birch) PFTs. Alder was separated from other low to tall shrubs because it hosts N-342 fixing actinomycetes in its root nodules and has significantly different tissue chemistry, 343 particularly higher leaf N concentrations. Development and evaluation of new alder N fixation 344 capabilities was beyond the scope of this paper, but ecosystem-scale N fixation rates in the alder-345 dominated AS plant community were increased in our simulations to ensure that simulated plant 346 growth in the community dominated by N fixers would not be N limited, as consistent with observations of an open N cycle in the AS community (Salmon et al., 2019a). 347

348 The new PFTs were parameterized using biomass measurements from the Kougarok 349 Hillslope site (Salmon et al., 2019b). Parameterization was focused on biomass rather than height 350 because canopy height in ELM is calculated from aboveground biomass using fixed allometric 351 parameters and is used primarily for calculating atmospheric roughness rather than directly 352 affecting C and nutrient cycling. Tissue allocation parameters (leaf to fine-root growth ratios and 353 stem to leaf growth ratios) were the primary parameters that were adjusted. Leaf maximum 354 photosynthesis rate (VCmax) is calculated in ELM using leaf N content (a static PFT parameter) 355 and the fraction of leaf nitrogen in the Rubisco enzyme (FLNR) parameter. Leaf N content was 356 parameterized using site measurements, and FLNR was adjusted so that growing season VCmax 357 matched literature values for Arctic PFTs (Bubier et al., 2011; Nash et al., 1983; Rogers et al., 358 2017; Williams & Flanagan, 1998). Specific leaf area for each PFT was parameterized using site 359 measurements. Rooting depth distribution in ELM follows the double-exponential formulation of Zeng et al., (2001), which uses two depth parameters. These parameters were adjusted based on 360 361 maximum rooting depth of arctic plant species reported by Iversen et al. (2015). Rooting depth is further constrained in the model by adjusting root depth distribution so it does not extend below 362 363 the depth to bedrock or deeper than the thickness of the simulated active layer.

Graminoids (including grasses, sedges, and rushes) are assumed to be deciduous or
annual plants in the default E3SM configuration, allowing all leaf and fine root biomass to
senesce each autumn and regrow in the spring. However, the majority of Arctic graminoids have
leaf and fine root tissues that persist for multiple growing seasons (Shaver & Laundre, 1997).

Therefore, graminoids in the new Arctic PFT configuration were set to be evergreen plants, with a leaf lifespan of two years (Shaver & Laundre, 1997) and a fine-root lifespan of approximately years (Sullivan et al., 2007). Forbs, including non-flowering vascular plants such as ferns and horsetails, which were more likely to be truly deciduous at the Kougarok Hillslope site, were separated from graminoids and remained deciduous in the updated model.

373 Many arctic plants allocate a high fraction of their growth to belowground tissues 374 (Iversen et al., 2015), and grow a relatively small amount of new leaf and fine-root tissue each 375 year, reflecting a conservative growth strategy consistent with short growing seasons (Thomas et 376 al., 2020). Thus, arctic PFTs were adjusted to maintain larger storage pools and express a lower 377 fraction of storage into tissue growth each year. In the original ELM configuration, non-woody 378 plants were limited to include only leaf, fine-root, and storage pools. The model was modified to 379 add rhizome tissues, treated as living coarse-root tissue, to graminoids and forbs (woody shrub 380 PFTs in the model already have associated coarse roots). Allocation to coarse root and rhizome 381 tissues were parameterized using site estimates of rhizome and belowground stem biomass.

Bryophytes and lichens were introduced as separate PFTs. While nonvascular plants and lichens differ in many important ways from vascular plants, including in their water transport, transpiration, and photosynthesis capabilities, development of new nonvascular-specific processes was beyond the scope of this study. Instead, nonvascular PFTs were parameterized as nonwoody plants with very low root biomass and photosynthesis parameters were set based on previous measurements of moss and lichen photosynthetic capabilities (Nash et al., 1983; Williams & Flanagan, 1998).

Fine-root respiration in ELM is a function of fine-root N concentration and also depends on temperature through a Q10 relationship. The default model does not allow living roots to become dormant during the winter. To prevent fine-root respiration from depleting plant C reserves over the long winter season, the model was modified to allow fine roots to become dormant when soil temperatures were below -1 °C (Monson et al., 2006). In a dormant state, fine-root respiration was reduced to 5% of its non-dormant rate.

395

Table 2: PFTs and key parameters. FLNR: Fraction of nitrogen in Rubisco. Model max rooting depth is defined as depth that 99% of root biomass is above, calculated from the rooting depth parameters. Data sources used to determine the new value of each parameter are shown as letters in the bottom row with citations in the footnote.

PFT	Root:le af allocati on ratio	Stem:lea f allocatio n ratio	Coarse root:ste m ratio*	Leaf C:N	Fine root C:N	FLNR	Specific leaf area (cm ² g C ⁻¹)	Leaf habit	Rooting depth params (m ⁻¹)	PFT max rooting depth (cm)
Default PFTs (Default PFTs (Simulations 1 and 2)									
Broadleaf deciduous boreal shrub	2.0	0.2	0.3	25	42	0.1365	300	Deciduous	7.0, 1.5	260
C3 arctic grass	2.0	N/A	N/A	25	42	0.1365	300	Deciduous	11.0, 2.0	200
New PFTs (Simulation 3)										

Lichen	0.2	N/A	N/A	84	42	0.435	300	Evergreen	400, 800	0.98
Bryophyte	0.1	N/A	N/A	55	42	0.485	300	Evergreen	100, 200	3.9
Evergreen dwarf shrub	3.0	0.1	1.0	44	58	0.0755	134	Evergreen	30, 13	30
Deciduous dwarf shrub	1.5	0.2	0.5	27	58	0.1365	213	Deciduous	13, 10	42
Deciduous low shrub	1.4	0.2	0.5	31	58	0.1365	201	Deciduous	13, 10	42
Deciduous low to tall shrub	1.3	0.2	0.5	22	58	0.1365	237	Deciduous	13, 10	42
Alder shrub	0.25	0.5	0.6	21	58	0.1365	275	Deciduous	13, 10	42
Forb	1.5	N/A	0.1*	30	58	0.2	300	Deciduous	11, 9	47
Graminoid	4.0	N/A	0.1*	27	75	0.09	165	Evergreen	11, 9	47
Data source for new parameteriza tion	a, b	a	с	a	b	d	a	N/A	b	b

400 *For graminoids and forbs, rhizome-leaf ratio is shown in the coarse root/stem ratio column

401 a. (Salmon et al., 2019b)

402 b. (Salmon et al., 2019c)

403 c. (Shaver & Chapin, 1991)

404 d. Bubier et al. (2011); Nash et al. (1983); Rogers et al. (2017); Williams & Flanagan (1998)

405 2.4 Model simulations

406 ELM simulations were conducted for the Kougarok Hillslope site using meteorological 407 driving data from the Scenarios Network for Alaska and Arctic Planning (SNAP) downscaled

409 2018). Model simulations were spun up using 200 years of accelerated decomposition, followed
410 by 600 years of regular spinup (Koven et al., 2013; Thornton & Rosenbloom, 2005). The SNAP

forcing included the historical period from 1970 to 2005, extended through 2100 using the

411 RCP8.5 scenario. Spinup and historical simulations were conducted beginning in 1850, with

413 periods prior to 1970 simulated by repeating the historical period of the SNAP forcing. SNAP

414 meteorology was bias corrected to match DAYMET precipitation at the site, with winter

415 precipitation reduced by a factor of 2 to better match estimates of snow depth and spring

416 snowmelt date at the site. Atmospheric CO_2 forcing used historical time series data starting in

417 1765 and extending through 2100 using the RCP8.5 scenario.

418 All simulations were repeated using three levels of model simulations representing a

419 progression from the default model configuration of ELM within E3SM to a specific

420 parameterization of Arctic PFTs within an updated ELM (Figure 4). Simulation 1 used grid cell

421 data from a global E3SM configuration, including the fractional area of E3SM PFTs assigned to 422 the grid cell containing the Kougarok Hillslope site in global simulations. This simulation did not

- 422 the grid cell containing the Kougarok Hillslope site in global simulations. This simulation did not 423 distinguish between different plant communities on the Kougarok Hillslope, but instead used a
- 424 single point simulation to represent the entire area. Simulation 2 used default E3SM PFT
- 425 definitions combined with adjusted depth to bedrock for plant communities with shallow rocky
- 426 layers to represent the role of abiotic soil factors in driving site differences, and adjusted the
- 427 relative areas of the broadleaf deciduous boreal shrub and C3 arctic grass PFTs to reflect the
- 428 observed spatial coverage of shrub and non-shrub PFTs across Kougarok Hillslope plant
- 429 communities. Areas of all non-shrub PFTs, including graminoids, forbs, lichens and bryophytes,
- 430 were included in the C3 arctic grass coverage fraction for this simulation. Simulation 3, the most
- 431 site-specific level, used the new arctic PFT definitions and parameterizations based on the
- 432 vegetation types present at the site, including measured soil depths in communities where soil
- 433 was underlain by rocky layers (Table 2). While relative spatial areas of PFTs varied among plant
- 434 communities, the parameters of each PFT were the same regardless of plant community.
- 435

436



437 Figure 4: Relative areas of PFTs for three model configurations. (a): Downscaled E3SM grid

- 438 *cell and E3SM PFTs (Simulation 1); (b): E3SM PFTs with community-specific fractions of*
- 439 shrub, grass, and non-vegetated areas (Simulation 2); (c): Measured areas of Arctic PFTs
- 440 *(Simulation 3). Dashed outlines show which arctic PFTs were combined into the PFT areas in* 441 *Simulation 2*
- 441 *Simulation 2.*

442 3 Results:

443 3.1 Contemporary vegetation biomass patterns



445 Figure 5: Smoothed histograms of vegetation biomass distribution, color coded by PFT. (a):

- 446 Observed PFT biomass. (b): E3SM grid cell with default PFTs and single soil depth (Simulation
- 447 1). (c): E3SM PFTs with varying soil depths and relative areas of shrubs and grasses
- 448 (Simulation 2). (d): Arctic PFTs with varying soil depths (Simulation 3).

449

444

450 451 Distributions of measured PFT biomass among plots highlighted the diversity of PFTs 452 present along the Kougarok Hillslope gradient (Fig. 2) as well as the variability in their 453 contributions to plot biomass (Fig. 5a). Measurements showed that various dwarf and low shrub 454 PFTs contributed a range of biomass values across measurement plots, from less than 100 g C m ² to over 1000 g C m⁻². Low to tall deciduous non-alder shrubs also tended to make small 455 456 contributions (less than 1000 g C m⁻²) to total plot biomass despite their larger stature. Only alder shrubs dominated plots with high biomass of greater than 1500 g C m⁻², with the most productive 457 alder plots dwarfing other PFTs with up to 6000 g C m⁻². Forbs and graminoids ranged up to 458 459 1000 g C m⁻². Nonvascular PFTs, including bryophytes and lichens, generally had low total biomass but were widespread among plots. 460

461 Distributions of simulated PFT biomass (averaged from years 1990-2010, following 462 spinup and historical period simulations) across modeled plant communities showed how adding 463 information to the model improved both diversity and biomass of modeled relative to observed 464 PFTs. Simulations using original E3SM PFTs (Simulation 1; Fig. 5b) showed how a grid-cell-465 level simulation with only two PFTs led to underestimates of biomass variability across plots. 466 These simulations overestimated shrub biomass compared to measurements and missed the 467 significant fraction of plots with small amounts of shrub biomass or moderate amounts (> 500 g $C m^{-2}$) of non-shrub biomass. When variations in soil depth to bedrock and relative shrub and 468 469 graminoid area were taken into account (Simulation 2; Fig. 5c), simulated variability in shrub 470 biomass was improved relative to observations, with some low-biomass plots represented. 471 However, Simulation 2 still overestimated the prevalence of shrub biomass in the 1000-2000 g C 472 m⁻² range while not reproducing high-biomass alder plots. Simulated biomass using new ELM 473 arctic PFTs parameterized with site-level observations (Simulation 3; Fig. 5d) had distributions 474 of PFT biomass that were more consistent with observations for nonvascular PFTs, graminoids, 475 forbs, and most shrubs. However, the modeled biomass was skewed somewhat low and 476 underestimated biomass of forbs and dwarf shrubs in communities where they reached higher biomass (in the 500-1200 g C m^{-2} range). The model also failed to reproduce the highly-477 productive alder sites, with modeled alder biomass occurring mostly in the 1500-2000 g C m⁻² 478 479 range compared to observed alder biomass of up to 6000 g C m^{-2} .

480 Patterns of biomass were clarified by separating the study area into representative plant 481 communities for comparison with modeled plant communities (Figure 6). Measured biomass in 482 the DLST community at the summit and crest of the hillslope was dominated by lichens, with 483 evergreen dwarf shrubs contributing a small amount despite their larger fractional cover (Fig. 484 6a). The BEL community at the shoulder of the hillslope (Fig. 6b) also had a large fraction of 485 biomass made up by lichens, but dwarf and low shrubs made up a larger fraction of aboveground 486 biomass, and also contributed to a substantial amount of belowground biomass. The tall-statured 487 AS community, predominantly on the upper backslope, had the highest biomass of any 488 community due to dominant alder shrubs (Fig. 6c). The WBT community, also on the backslope, 489 was dominated by deciduous shrubs, with biomass divided relatively evenly between low and 490 low to tall shrubs (Fig. 6d). The ASV community on the lower backslope and footslope had 491 lower biomass of shrubs than AS and a higher fine-root biomass relative to above ground biomass 492 (Fig. 6e). Biomass of the TT community on the footslope was dominated by graminoids, 493 specifically tussock-forming sedges. Biomass in this community was largely belowground, with 494 fine roots making up a large fraction of total biomass (Fig. 6f).

495 Model simulations using default E3SM grid cell PFTs for the grid cell containing the 496 Kougarok Hillslope site (Simulation 1) were dominated by deciduous shrubs. This pattern was 497 most consistent with the AS and WBT plant communities but did not reflect the diversity of 498 shrub growth patterns in those communities. The other communities did not match the E3SM 499 grid cell pattern well, including DLST, where the default model greatly overestimated shrub 500 biomass, and the ASV and TT communities, where the default model underestimated the 501 coverage and biomass of graminoids. Simulations with community-specific soil depths and 502 relative cover of grasses and shrubs (Simulation 2) were somewhat improved relative to 503 observations, with improved model estimates of total biomass in the DLST and BEL 504 communities. However, these simulations greatly underestimated biomass in the AS community. 505 In addition, E3SM PFTs (Simulations 1 and 2) substantially underestimated the belowground 506 fraction of total biomass (including rhizomes and fine roots) in all plant communities except the 507 nonvascular-dominated DLST community, which had very low belowground biomass. 508 Simulation 3, with measurement-constrained tundra PFTs, corresponded well with observations, 509 although alder biomass in AS and lichen biomass in DLST were still underestimated.

510 Soil depth to bedrock in the model was an important control on vegetation biomass, as 511 evidenced by the contrast between Simulations 1 and 2. While soil depth for communities 512 underlain by rocky layers (DLST, BEL, and AS; Table 1) was set to measured values, active 513 layer thickness (the primary control on plant-available soil thickness in WBT, ASV, and TT) was 514 determined by ELM thermal-hydraulic calculations. Mean maximum active layer thickness simulated in ELM over the 1990-2010 period was 2.3 m, 4.6 m, and 12.6 m respectively for the 515 516 WBT, ASV, and TT communities. These depths were roughly an order of magnitude greater than 517 observed depths to frozen layers of 32-33 cm for those communities (Table 1).

518 519



521 Figure 6: Total biomass in each plant community. Panels a-f show vascular biomass and panels

- 522 g-l show nonvascular biomass. Aboveground biomass is shown as upward bars, and
- 523 belowground biomass (including PFT-specific rhizomes and pooled fine roots) is shown with
- 524 downward bars. Sim 1: E3SM grid cell data. Sim 2: E3SM PFTs with community-specific
- 525 shrub/grass relative areas and soil depth to bedrock. Sim 3: Arctic PFTs and community
- 526 composition. Note that simulations 1 and 2 lacked nonvascular PFTs. Colors in each bar
- 527 indicate the biomass of different PFTs. Error bars show standard deviation of measurements of
- 528 *each PFT. Note that vertical scales vary among panels.*
- 529

520

- 530 Comparing the biomass of individual PFTs between model simulations and 531 measurements highlighted the improvements from Arctic-specific PFT developments (Figure 7). 532 Individual shrub PFTs in Simulation 3 generally reproduced variations in biomass across plant 533 communities ($R^2 = 0.32$ and 0.7 for every every every every shrub and deciduous low shrub, respectively; only two data points were available for tall and alder shrubs; Fig. 7c-f). Simulation 534 535 2, by contrast, greatly underestimated biomass in the AS community leading to low correlation across communities (Fig. 7a; $R^2 = 0.002$). While the C3 arctic grass PFT in Simulation 2 did 536 537 capture most of the observed variability in nonwoody vascular biomass (Fig. 7b; $R^2 = 0.75$), nonvascular PFTs were not defined in that simulation. In Simulation 3, graminoid biomass 538 generally reproduced observations (Fig. 7g; $R^2 = 0.87$). Simulated forb biomass (Fig. 6h) was not 539 as well correlated with observations ($R^2 = 0.17$), although total biomass of forbs was low 540 compared to other PFTs. Simulated lichen and bryophyte biomass (Figs. 7j,i) both compared 541 542 fairly well with observations, with a higher correlation for lichens, which also made up more 543 total biomass ($R^2 = 0.61$ and 0.35 for lichens and bryophytes, respectively).
- 544



 545
 Obs Biomass (gC m⁻²)
 Obs Biomass (gC m⁻²)
 Obs Biomass (gC m⁻²)
 Obs Biomass (gC m⁻²)

 546
 Figure 7: Modeled and measured biomass of each PFT. Different symbols show the different

- 547 plant communities. Panels (a) and (b) show E3SM PFTs with site-specific soil depth and relative
- 548 areas (Simulation 2) compared with observed PFTs pooled into shrub, non-shrub, and
- 549 nonvascular groups. Panels c-j show new arctic PFTs (Simulation 3) compared with measured
- 550 biomass of each PFT. Deciduous dwarf shrubs are not shown because biomass was not

551 measured for that PFT. Observed values show the mean of two plots, with a bar showing the

range between the two measurements. Total measured nonvascular biomass is shown in orange
symbols in the C3 Arctic Grass panel (b).

554 3.2 Historical and projected biomass changes

555 Time series of vegetation biomass showed clear historical patterns with substantial differences among the three simulations (Figure 8). All simulations showed gradual biomass accumulation 556 over the historical period, followed by accelerating biomass accumulation from 2000 through 557 2080. However, different approaches to defining PFTs and communities drove large differences 558 559 in historical and projected biomass across the hillslope's plant communities. Shallow depth to rocky layers in DLST and AS (Table 1) caused both historical biomass and projected biomass 560 accumulation to be much lower in Simulation 2 than in Simulation 1. New, Arctic-specific PFTs 561 562 (Simulation 3) drove dramatically larger biomass in shrub-dominated ecosystems for simulation 563 3 versus 2. These increases were especially notable in AS and ASV where N limitation was alleviated by higher N fixation associated with the alder shrub PFT included in Simulation 3. 564

565



566

Figure 8: Time series of total community vegetation biomass for the three simulations. Vertical
line indicates transition from historic to future climate drivers.

569

570 Changes in the biomass of individual arctic PFTs over time showed varying patterns across 571 simulated PFTs and plant communities (Figure 9). Generally, biomass of mosses and lichens was

- less sensitive than that of vascular plants to changing climate and CO_2 concentrations, except in
- 573 the lichen-dominated DLST community where lichen biomass increased significantly from 2000-
- 574 2100. Low shrubs and graminoids had higher biomass growth responses than other PFTs in
- 575 communities containing significant biomass of both graminoids and shrubs such as TT and ASV.
- 576 This included alder in ASV, where it was eventually overtaken by low shrubs in terms of total
- 577 biomass. In the AS community, however, alder had strong projected growth that drove
- 578 community biomass accumulation from 2000-2100.



Figure 9: Time series of biomass of each PFT in Simulation 3 across the Kougarok Hillslope
gradient of plant communities.

582 4 Discussion:

579

583 Tundra ecologists have long known that the diversity of plant species and functional traits 584 across the Arctic tundra have important consequences for the cycling of energy, water, carbon 585 and nutrients (Bjorkman et al., 2018; Bliss et al., 1981; Chapin et al., 1996; Sturm et al., 2005; 586 Turetsky et al., 2012; Wielgolaski, 1972). By confronting a land surface model with site-scale 587 measurements of plant biomass and tissue traits, above- and belowground, across a range of plant 588 communities and functional types, we were able to identify deficiencies in the default model and 589 improve representation of both plant functional type diversity and total values of biomass, above-590 and belowground, across a gradient of tundra plant communities on the Seward Peninsula of 591 Alaska. Because it was limited to coarsely-defined boreal shrub and C3 arctic grass PFTs, the 592 default model configuration in ELM failed to reproduce the diversity of plant traits and growth 593 forms, which included several shrub forms, nonvascular lichens and bryophytes. Our model 594 improvements highlight the importance of representing the diversity of Arctic plant growth 595 forms, which have been previously identified as a challenge for traditional functional type 596 approaches (Thomas et al., 2019; Wullschleger et al., 2014). Averaging over variation in Arctic 597 PFTs has been shown to bias simulated biomass (Epstein et al., 2001), and our results were 598 consistent with this finding. Even for species that mapped easily onto existing model PFTs such 599 as low to tall shrubs and graminoids, the default model parameterization underestimated belowground biomass allocation, suggesting that current model simulations at global or pan-600 601 Arctic scales may underestimate belowground productivity despite overestimating the available 602 rooting zone in several communities. Because a large proportion of soil organic matter is root-603 derived (Jackson et al., 2017; Rasse et al., 2005), this could lead to bias in simulated soil carbon 604 stocks and should be revisited in large-scale model configurations. Previous analyses have shown that leaf photosynthetic traits are also often poorly parameterized in land surface models, 605 606 particularly for arctic vegetation (Rogers, 2014; Rogers et al., 2017).

607 The large contribution of nonvascular bryophytes and lichens to total biomass in several of the plant communities in this study (Fig. 5) highlights the need for integration of these 608 609 organisms into land surface models in the Arctic. Mosses, and particularly Sphagnum spp., play 610 important roles in high-latitude ecosystems, including buffering the soil from air temperature fluctuations and potential permafrost thaw, forming a barrier to surface water fluxes, and 611 612 influencing nutrient availability and ecosystem responses to fire (Beringer et al., 2001; Blok et 613 al., 2011; Gornall et al., 2007; Kellner, 2001; Turetsky et al., 2012). Lichens can contribute 614 significantly to C uptake and N fixation in arctic ecosystems (Crittenden & Kershaw, 1978; 615 Lange et al., 1998) and play important ecological roles including forming an essential part of the 616 caribou diet in the winter (Longton, 1997). While some large-scale models have begun to integrate nonvascular PFTs and their particular traits (e.g., Druel et al., 2019; Shi et al., 2020), 617 618 ELM has, until now, lacked specific capability for nonvascular arctic PFTs. In this study, 619 bryophytes and lichens were implemented within the existing PFT framework as nonwoody 620 plants with very low belowground biomass. However, this approach does not incorporate the 621 physiological differences that separate bryophytes and lichens from vascular plants, including 622 water transport and lack of stomatal control, and as a result likely underestimates the differences 623 in land-atmosphere energy and water fluxes in nonvascular-dominated communities compared to 624 vascular-dominated communities (Porada et al., 2016; Stoy et al., 2012). More model 625 improvements are needed to accurately represent bryophyte and lichen physiology in ELM. To 626 this end, Sphagnum physiological processes such as capillary wicking of water and coupling of photosynthetic rate to tissue water content are being developed in ELM for northern peatland 627 628 ecosystems (Shi et al., 2020), and these developments could be incorporated into arctic 629 bryophyte simulations in the future.

630 Our simulations suggested that potential for future biomass accumulation varied greatly 631 by plant community. Shrub-dominated communities as well as the graminoid-dominated TT 632 community had strong biomass responses to warming and increasing atmospheric CO₂ levels, with biomass increasing by up to a factor of two, or up to 2 kg C m⁻², through 2100. In the 633 634 shallow-soil, lichen-dominated DLST community, total biomass accumulation was low due to a 635 combination of PFT traits that limited growth and shallow soils that limited water and nutrient 636 availability. However, our simulations greatly overestimated active layer thickness in the three communities underlain by deeper soils. This could have biased the results toward greater growth 637 638 potential in those communities by overestimating potential maximum rooting depth and access to 639 water and nutrients. Even so, our simulated active layer thicknesses of greater than 2 m were 640 consistent with previous large-scale model simulations in the Seward Peninsula region (Koven et 641 al., 2011). These results highlight the importance of including landscape-scale variation in both 642 abiotic factors, including lateral thermal-hydraulic processes, and plant communities in 643 simulations of Arctic biogeochemistry. Simulations using a single average community across the 644 grid cell omitted both the high and low ends of the biomass response distribution, which could 645 introduce bias into larger-scale simulations of Arctic responses to global changes. Model 646 overestimates of active layer thickness suggest that additional work is needed to improve 647 permafrost thermal-hydraulic process representation in order to reduce potential bias in plant 648 growth for permafrost-affected plant communities. 649 The enhanced vegetation growth in our simulations of arctic ecosystems under warming

climate and increasing CO₂ concentrations is consistent with previous vegetation measurements (Myers-Smith et al., 2019), model simulations (Koven et al., 2011; McGuire et al., 2012) and evidence from remote sensing (Jia et al., 2003). The magnitude of biomass gains over the 21^{st}

century in Simulation 1 was approximately 1.7 kg C m⁻², which was within the range of multiple 653 models applied to the Arctic region (Ito et al., 2016), and was consistent with an estimated 20% 654 655 increase in aboveground phytomass in circumpolar Arctic tundra from 1980-2010 (Epstein et al., 656 2012). Taking into account heterogeneity in soil depths and plant communities (Simulation 3) greatly expanded the range of biomass changes, from a gain of only 0.158 kg C m⁻² in DLST to 657 an increase of approximately 2 kg C m⁻² in the AS and WBT communities. This variability is 658 659 consistent with more detailed measurements and model simulations of changes in arctic 660 ecosystems. Myers-Smith et al. (2020) suggest that observed "greening" of the Arctic is complicated by heterogeneity in ecological and physical factors. Shaver & Chapin (1991) noted 661 662 the large variation in biomass and primary production among tundra vegetation types within a relatively small area, and Euskirchen et al. (2009) found that biomass change over the 21st 663 664 century in arctic ecosystems varied substantially between shrub- and sedge-dominated tundra 665 types. Epstein et al. (2001) found that multiple arctic PFTs were necessary to accurately 666 represent biomass and primary production in tundra ecosystems. Landscape factors such as nutrient availability, water flow, disturbance history, growing season length, and presence of 667 668 competitors can have important effects on shrub expansion (Bhatt et al., 2017; Myers-Smith et 669 al., 2011, 2020). Similarly, Elmendorf et al. (2012) found that responses of different arctic PFTs 670 to warming varied with moisture and permafrost status, and Lara et al. (2018) showed how fine-671 scale variations underpin larger-scale patterns of change in arctic landscapes. Our results show 672 how such fine-scale variability in abiotic site factors and plant communities can drive different 673 biomass growth patterns under climatic warming and increasing CO₂ concentrations within a 674 land surface model.

675 The AS plant community stood out in our simulation results, highlighting the counteracting effects of biotic and abiotic factors in driving model outcomes. The AS community 676 had shallow soils (Table 1), and as a result when soil depth differences but not arctic PFT 677 678 parameterizations were included (Simulation 2) the model simulated less biomass in AS than in 679 the E3SM grid cell (Simulation 1). However, in observations of alder shrubs the AS community 680 had by a large margin the highest biomass of any Kougarok Hillslope plant community. Only 681 when differences in arctic plant traits were incorporated, including higher wood allocation and 682 lower fine-root allocation of alders as well as the alleviation of N limitation in the alder-683 dominated community (Simulation 3), was the model able to reproduce the observed pattern. 684 Even with these changes, the model somewhat underestimated total alder biomass in the AS 685 community, suggesting that additional factors might be missing from the current model 686 configuration. Previous measurements at the Kougarok site showed that alders living in the AS 687 community have trait differences from alders in the ASV community, including taller growth 688 forms, denser shrub-dominated patches, and different rates of N fixation (Salmon et al., 2019a), 689 however model simulations treated them as identical PFTs. Hydrological drainage patterns 690 differed between the AS and ASV communities, with ASV more likely to retain water, 691 potentially stressing alder growth. Leaf stoichiometry also suggested that P availability was 692 higher in the AS community. These hydrological and nutrient factors were not included as cross-693 community differences in the model configuration for the present study. In addition, N fixation 694 in ELM is empirical rather than process-based, and does not include nodulation, P limitation, or 695 differences in N availability to different PFTs. Improvements to the N fixation model might 696 allow more accurate simulation of the dynamics of N-fixing alder shrubs. For example, 697 associating high N fixation rates directly with alder shrubs and giving that PFT preferential

access to the newly-fixed N could allow an increase in alder shrub productivity without
 introducing bias in productivity estimates for other plant types co-occurring with alder.

700 This study focused on plant communities in one intensive study area on the Seward 701 Peninsula of Alaska in the low Arctic in close proximity to latitudinal treeline. As a result, it likely underestimates the full diversity of vegetation traits across the Arctic region. Despite this 702 703 limitation, the Kougarok Hillslope site adds to our understanding of tundra plant traits, which 704 along with other Arctic environmental measurements are often quantified in only a few locations 705 in the world (Bjorkman et al., 2018; Metcalfe et al., 2018; Virkkala et al., 2019). The PFTs 706 identified in our study matched well with trait-based classifications, particularly size-related 707 traits, identified as covering most of the variability in Arctic plant traits (Thomas et al., 2019), 708 including more accurate ratios of belowground biomass allocation observed in tundra plant 709 communities (Iversen et al., 2015). The plant communities in our study area included multiple 710 shrub-dominated community types (AS, WBT) with low or tall shrubs that are typical of the low 711 Arctic and less common in the high Arctic. Understanding and accurately modeling the traits of 712 shrub-dominated plant communities is important for predicting the future of the Arctic, where 713 shrub expansion is an important ongoing process with significant effects on both 714 biogeochemistry and biophysical land-atmosphere interactions (Bonfils et al., 2012; Euskirchen et al., 2009; Tape et al., 2006; Wilcox et al., 2019). However, a full understanding and accurate 715 716 prediction of Arctic responses to warming climate will require sampling across a broad range of 717 climates and plant communities (Thomas et al., 2020).

718 Along with increases in total biomass, our simulations projected changes in relative 719 biomass of different PFTs over the 21st century (Fig. 9). In the TT community, the model 720 predicted an increase in graminoid biomass overcoming shrub PFTs. Graminoids and low 721 deciduous shrubs were also projected to increase relative to other PFTs in the ASV community. 722 These projections reflect differences in biomass accumulation potential, but omit some processes 723 that could be important drivers of future changes. First, the version of ELM used in our 724 simulations does not represent height-structured competition for light among PFTs or the impact 725 of increased leaf litter on lichens and bryophytes. As biomass increases in the future, low-726 statured vegetation such as dwarf shrubs, lichens and bryophytes could be shaded out by taller 727 shrubs, graminoids and forbs (Elmendorf et al., 2012a; Myers-Smith et al., 2011; M. D. Walker 728 et al., 2006). Our simulations likely overestimate the potential future growth of short-statured 729 vegetation by omitting this effect. Ongoing developments to incorporate height-structured light 730 competition among PFTs in ELM will help to address this issue in the future (Koven et al., 731 2020). Second, our simulations of historical and future changes in vegetation biomass assumed 732 constant relative areas of different PFTs within each plant community and did not calculate 733 changes in the relative areas of the plant communities due to either climate change or 734 disturbances. As a result, our results may underestimate the potential for future biomass 735 accumulation connected with shrub expansion. For example, the area of the AS plant community 736 on the Kougarok Hillslope has increased over recent decades (Salmon et al., 2019a). The much 737 higher biomass of the AS community compared to other communities at the study site suggests a 738 high potential for biomass accumulation under future shrub expansion. This highlights the need 739 for model simulations of the Arctic region to incorporate either projections of changes in plant 740 community areas or direct simulations of changing species cover using dynamic vegetation and 741 demographic processes (Druel et al., 2019; Fisher et al., 2018). 742 Other ecosystem and land surface models have been developed for Arctic ecosystems,

with varying capabilities and levels of complexity. Arctic-specific models have been designed to

744 represent plant communities and their variability at a high level of detail. For example, the TEM 745 model (Euskirchen et al., 2009) was designed specifically for improved representation of high-746 latitude processes. It includes 26 high-latitude PFTs including variations in parameterizations for 747 different ecosystems. Land surface models similar to ELM tend to be limited in the specificity of 748 their PFTs due to the necessity of representing ecosystems across continental to global spatial 749 scales (Wullschleger et al., 2014). However, progress has been made in parameterizing Arctic-750 specific vegetation types in other models. For example, northern shrubs and mosses were added 751 to the ORCHIDEE land surface model, allowing more realistic simulation of vegetation spatial 752 distributions in boreal regions (Druel et al., 2019). Our results underscore the value of such 753 activities and suggest that better representation of plant diversity in Arctic ecosystems will 754 improve the quality of Earth system model projections of Arctic feedbacks to a changing climate. 755 Rich emerging datasets of Arctic vegetation traits and plant-soil interactions (Bjorkman et al., 756 2018; Iversen et al., 2015; Thomas et al., 2020) provide opportunities to further improve models 757 such as ELM by targeting key processes including PFT-specific N fixation patterns, root 758 function, vegetation-snow interactions, and plant species demography.

⁷⁵⁶ function, vegetation-snow interactions, and plant species demog

759 5 Conclusions:

760 We used intensive field measurements to develop updated model PFTs and parameters 761 representing the diversity of plant functional types observed in the Seward Peninsula of Alaska, 762 USA. New PFTs included forbs, nonvascular plants, and multiple shrub types with different 763 potential heights and leaf habits. Updated PFTs drove differences in contemporary and projected 764 biomass and improved representation of the variability in biomass across different plant 765 communities in the study area, particularly for highly productive alder shrublands. Updated 766 parameterizations also improved simulations of belowground biomass allocation, which was 767 underestimated in the default model. When projected into future climate conditions (RCP 8.5 768 through 2100), updated arctic PFTs showed increased vegetation C storage, especially in shrub-769 dominated communities. Our results highlight the importance of representing the diversity of 770 vegetation types and abiotic soil factors in modeling Arctic ecosystems. 771

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Arctic Data Repository as cited in the manuscript. Forcing data, model output, and scripts used

for model configuration and data analysis are also archived at the NGEE Arctic Data Repository

786 (Sulman et al., 2020).

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¹¹⁴⁴ 8 Supplementary figures and tables

Figure S1. Comparison between raw data in Berner et al 2015 (grey) and NGEE Arctic destructive harvests of tall shrub species (red).





1149 Table S1. Ratio of rhizome biomass to aboveground biomass in Shaver & Chapin 1991

	Rhizome Bio	Rhizome Biomass : Aboveground Biomass				
	Tussock Tundra	Tussock Tundra Shrub				
PFT	Community	Community	Community			
Graminoid	0.91	0.36	1.40			
Deciduous	1.51	1.07	1.36			
Evergreen	1.41	0.17	0.88			
Forb	0.89	0.51	NA			
All vascular	1.29	1.05	0.99			

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1152 Table S2. Fine root turnovers in arctic literature

Community	Fine root turnover (years)	Notes
AS	1.33	Sequential soil cores collected in interior AK Alder- Balsam poplar stand (Ruess et al., 1996)
BEL	1.56	From sequential cores in a dry heathland in the Netherlands (evergreen dwarf species) (Aerts et al., 1992)
DLST	1.56	From sequential cores in a dry heathland in the Netherlands (evergreen dwarf species) (Aerts et al., 1992)
TT	3.13	From fine root biomass pools and minirhizotrons in tussock tundra at Toolik (Sullivan et al., 2007). (Shaver & Billings, 1975) estimates from Barrow have turnover time of 4 years but for wet sedge tundra. Tundra at our site is more similar to Toolik plant community so Sullivan's is more applicable
ASV	2.23	Average of Ruess et al. (1996) Alder-Balsam popular and Sullivan et al. (2007) tussock tundra

		number
WBT	1.33	Ruess et al. (1996), sequential soil cores collected
		In merior AK Alder-Daisani popiai stand

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57	Table S3. Turnov	er of stems.	calculated from	aboveground	stems and apr	olied to rhizomes
		, -				

Community	PFT	Stem turnover (years)
AS	Evergreen dwarf shrub	26.55
AS	Deciduous low shrub	25.72
AS	Alder shrub	100.02
AS	Low to tall deciduous birch	29.78
ASV	Evergreen dwarf shrub	13.96
ASV	Deciduous low shrub	22.14
ASV	Alder shrub	80.30
ASV	Low to tall deciduous willow	42.47
WBT	Evergreen dwarf shrub	9.58
WBT	Deciduous low shrub	22.97
WBT	Low to tall deciduous birch	21.73
WBT	Low to tall deciduous willow	92.11
BEL	Dwarf evergreen shrub	24.63
BEL	Low deciduous shrub	21.62
TT	Dwarf evergreen shrub	13.18
TT	Low deciduous shrub	13.81
ТТ	Low to tall deciduous willow	33.6
DLST	Dwarf evergreen shrub	6.25

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