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## Understory plant diversity and composition across a postfire tree density gradient in a Siberian Arctic boreal forest

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1	Understory plant diversity and composition across a post-fire tree density
2	gradient in a Siberian Arctic boreal forest
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## 19 Abstract

20 Cajander larch (Larix cajanderi Mayr.) forests of the Siberian Arctic are experiencing 21 increased wildfire activity in conjunction with climate warming. These shifts could affect post-22 fire variation in the density and arrangement of trees and understory plant communities. To 23 better understand how understory plant composition, abundance, and diversity vary with tree 24 density, we surveyed understory plant communities and stand characteristics (e.g., canopy cover, 25 active layer depth, and soil organic layer depth) within 25 stands, representing a density gradient 26 of similarly-aged larch trees that established following a 1940 fire near Cherskiy, Russia. 27 Understory plant diversity and mean total plant abundance decreased with increased canopy 28 cover, which was also the most important variable affecting individual species' abundances. In 29 general, tall shrubs (e.g., *Betula nana* subsp. *exilis*) were more abundant in low-density stands 30 with high light availability, and mosses (e.g., *Sanionia* spp.) were more abundant in high-density 31 stands with low light availability. These results provide evidence that post-fire variation in tree 32 recruitment affects understory plant community composition and diversity as stands mature. 33 Therefore, projected increases in wildfire activity in the Siberian Arctic could have cascading 34 impacts on forest structure and composition in both overstory and understory plant communities. 35 Keywords: Cajander larch, Larix cajanderi, Betula nana subsp. exilis, wildfire, disturbance

## 36 Introduction

37 Rapid rates of global change make boreal forests particularly susceptible to forest loss 38 and/or transition to novel forest conditions (Johnstone et al. 2010; Scheffer et al. 2012). Boreal 39 forests are warming faster than the global average (IPCC 2013) and are experiencing 40 concomitant increases in fire activity (Shvidenko and Schepaschenko 2013), insect outbreaks 41 (Kharuk et al. 2017), and permafrost degradation (Turetsky et al. 2019). These altered 42 disturbance regimes often lead to a reorganization of forest composition and structure compared 43 to that found prior to the disturbance. These shifts could be especially important depending on how they impact understory plant species diversity and composition (De Grandpré et al. 1993: 44 45 Hart and Chen 2006; Jean et al. 2017) because the understory accounts for the majority of plant diversity (Turetsky et al. 2012; Gilliam 2007). Further, the understory community strongly 46 47 influences nutrient cycling and net primary productivity (Nilsson and Wardle 2005; Campioli et al. 2009), permafrost stability (Turetsky et al. 2012), and fuelbed characteristics for fires 48 49 (Sofronov and Volokitina 2010). Because of the important role of understory plant communities 50 in boreal forests, it is important to understand how disturbance-mediated shifts in overstory 51 structure and composition are related to changes in understory vegetation. 52 In boreal forests, patterns of tree regeneration following fires and other disturbances are 53 the result of complex interactions between many factors, including soil burn severity (Sofronov 54 and Volokitina 2010; Alexander et al. 2018), seed source availability (Cai et al. 2013), abiotic 55 conditions (Sofronov and Volokitina 2010; Johnstone et al. 2010; Cai et al. 2013), and 56 competitive interactions with other plant species (Nilsson and Wardle 2005; Doležal 2004; Hart 57 and Chen 2006). For example, while fire is required to improve seedbed conditions for many 58 boreal tree species (Sofronov and Volokitina 2010; Alexander et al. 2018), increases in fire

59 severity, extent, and frequency can decrease tree regeneration by reducing local seed source 60 availability (Cai et al. 2013). This is especially important for non-serotinous species like larch 61 (Larix spp. Mill.) or white spruce (Picea glauca (Moench) Voss) that rely on wind dispersal of 62 seeds from surviving mature trees within burned areas or nearby unburned forest for post-fire 63 tree recruitment (Greene and Johnson 2000). In forests where seed source availability is low or 64 when soil burn severity is not high enough to promote tree regeneration, forest loss or declines in 65 tree recruitment may occur, resulting in lower-density forests or conversion to grass or shrub-66 dominated ecosystems (Sofronov and Volokitina 2010; Scheffer et al. 2012; Cai et al. 2013; 67 Alexander et al. 2018). In contrast, where seed availability is high and fires reduce the depth of 68 the soil organic layer (SOL) enough to expose mineral soil seedbeds, high-density forests may 69 develop (Alexander et al. 2018) or compositional shifts may occur (e.g., Johnstone et al. 2010). 70 Because the majority of tree recruitment in boreal forests occurs within the first decade after fire 71 (Johnstone et al. 2004), the initial patterns of tree recruitment resulting from these interacting 72 factors can affect forest composition and structure for decades. 73 The variation in tree density that arises due to differences in post-fire recruitment and 74 seedling survival may affect and interact with resource availability and heterogeneity to 75 influence understory plant communities. Throughout the post-fire recovery period, resource 76 availability is often a strong driver of species richness and cover in young and mature boreal 77 forests (Bartels and Chen 2010; Kumar et al. 2018). Lower-density boreal forests with more open 78 canopies tend to have increased light availability in the understory, warmer microclimates, 79 decreased coniferous leaf litter, and increased nutrient availability relative to closed-canopied 80 forests (De Grandpré et al. 1993; Hart and Chen 2006; Ma et al. 2016). For example, in both

81 North American boreal forests and the Dahurian larch (*Larix gmelinii* (Rupr.) Rupr.) forests of

82 northeast China and central Siberia, understory plant communities in areas with low tree density 83 typically have higher diversity and are dominated by shrubs and early-successional, shadeintolerant forbs (Kobak et al. 1996; Hart and Chen 2006; Ma et al. 2016). In contrast, understory 84 85 plant communities in higher-density forests with lower resource availability typically have lower 86 diversity and are dominated by bryophytes and shade-tolerant forbs (Hart and Chen 2006; Ma et 87 al. 2016). While resource availability can be an important driver of understory plant 88 communities, resource heterogeneity also becomes important during later stages of forest 89 development (Bartels and Chen 2010). This can arise through increased substrate diversity 90 (Kumar et al. 2018), heterogeneity of light and soil resources (Bartels and Chen 2010), and 91 microtopography, particularly on sites with permafrost soils where freeze-thaw-induced 92 microtopographic patterning can increase species richness (Zyryanova et al. 2007). Thus, 93 variation in both resource availability and heterogeneity in similarly-aged forest stands that 94 develop with different densities could lead to differentiation in the diversity and composition of 95 understory plant communities.

96 Our primary goal was to investigate how understory plant species diversity and 97 composition change across a gradient of tree density in monodominant Cajander larch (Larix 98 *cajanderi* Mayr.) forests overlaying continuous permafrost in the northeast Siberian Arctic. We 99 studied these patterns in a ~20-km<sup>2</sup> Cajander larch forest, where similarly-aged stands developed 100 with different densities following a 1940 wildfire. As fire activity increases throughout the 101 region (Shvidenko and Schepaschenko 2013; Ponomarev et al. 2016), associated changes in 102 forest structure and composition are important to understand because of their potential influences 103 on ecosystem processes. For instance, reduced tree cover and expansion of shrubs in previously 104 forested areas following fires can lead to reduced aboveground carbon storage (Alexander et al.

105 2012), increased wintertime albedo (Loranty et al. 2014), and increased active layer depth 106 (Loranty et al. 2018). We asked how understory plant community diversity and composition vary 107 with changing stand characteristics and abiotic conditions across the larch density gradient. We 108 expected increased abundance of shrubs and other vascular plants in low-density stands with 109 lower canopy cover and increased active layer depth, and increased moss abundance in higher 110 density stands with decreased canopy cover and cooler soils. Together, we expected these shifts 111 in stand characteristics to lead to variation in understory plant community composition across the 112 larch density gradient, with the highest diversity of understory plants in low-density stands with 113 the greatest light availability (Bartels and Chen 2010).

### 114 Methods

#### 115 Study Region

116 In 2016, we investigated understory plant communities within a ~20 km<sup>2</sup> area burned in 117 1940, approximately 2 km from the Northeast Science Station in Cherskiy, Sakha Republic, 118 Russia (68.76 °N, 161.46 °E; Figures 1 and 2). This wildfire occurred just east of the Kolyma 119 River, approximately 130 km south of where the river enters the Arctic Ocean. The mean annual temperature of this region is -10.5 °C, with cold winters (average winter temperature = -31.3 ° 120 121 C) and mild summers (average summer temperature = 10.9 °C); mean annual precipitation is 122 228 mm (Cherskiy Meteorological Station, https://rp5/rul/Weather archive in Cherskiy). 123 Forests in this region are composed of Cajander larch, a deciduous needle-leaf conifer that is 124 wind-dispersed with masting events every 2-3 years and no seed dormancy (Abaimov 2010). 125 Mean tree height ranges from 4-8 m in early- to late-successional stands near Cherskiy 126 (Alexander et al. 2012). While Cajander larch as old as 878-885 years old have been identified in 127 central Siberia (Abaimov 2010), most trees sampled near Cherskiy are < 200 years old

128	(Alexander et al. 2012). This species has a shallow root system and can survive very cold air and
129	soil temperatures, making it well-adapted to growth on permafrost soils (Abaimov 2010).
130	Cajander larch typically require fire to reduce both competition (Matveeva and Matveev 2008;
131	Doležal 2004) and SOL depths for successful establishment (Zyryanova et al. 2007; Sofronov
132	and Volokitina 2010; Shorohova et al. 2009; Alexander et al. 2018), with very little
133	establishment in the absence of fire. Most fires (50 - 60 %) in northeast Siberia are stand-
134	replacing (Krylov et al. 2014) surface fires that cause larch mortality through damage to roots
135	(Sofronov and Volokitina 2010; Volokitina 2015), leaving few to no surviving trees within the
136	burn perimeter. Larch trees regenerate in a single cohort within the first few years after these
137	stand-replacing fires, leading to the development of even-aged cohorts (Shorohova et al. 2009).
138	While fire return intervals in Cajander larch forests historically ranged from 80-300 years
139	(Ponomarev et al. 2016), the frequency, extent, and prevalence of stand-replacing fires is
140	increasing in the region (Shvidenko and Schepaschenko 2013; Ponomarev et al. 2016).
141	Understory vegetation in these Cajander larch forests is composed of tall (typically > 1
142	m) and short (typically $< 1$ m) shrubs, forbs, grasses, lichens, and mosses. The most common tall
143	shrubs include dwarf birches (Betula nana subsp. exilis (Sukaczev) Hultén and B. divaricata
144	Ledeb.) and willows (Salix spp. L.). Common short shrubs include bog blueberry (Vaccinium
145	uliginosum L.), lingonberry (V. vitis-idaea L.), and bog Labrador tea (Rhododendron
146	tomentosum Harmaja). Other understory species include forbs such as bog wintergreen (Pyrola
147	asarifolia subsp. asarifolia Michx.) and arctic sweet coltsfoot (Petasites frigidus (L.) Fr.),
148	grasses like narrowspike reedgrass (Calamagrostis stricta (Timm.) Koeler), sedges like
149	cottongrass (Eriophorum spp. L.), mosses like aulacomnium moss (Aulacomnium palustre
150	(Hedw.) Schwaegr.) and wooly feather moss (Tomentypnum nitens (Hewdw.) Loeske), and

151 lichens like common frecklepelt (*Peltigera aphthosa* (L.) Willd.). A complete list of

nomenclature for the species identified in this study is available in Table S1.

153 Study Design

154 Following the 1940 stand-replacing fire, forest stands within the fire perimeter developed 155 with varying tree densities (83 - 42,000 stems/ha). This gradient in tree density likely originated 156 from variation in initial post-fire conditions related to soil burn severity, seed source availability, 157 and additional biotic and abiotic factors affecting seed germination and seedling survival, such as 158 weather during the post-fire growing seasons (Sofronov and Volokitina 2010; Alexander et al. 159 2012, 2018; Cai et al. 2013). The stands are even-aged with most trees originating between 10 160 and 15 years after the 1940 wildfire, and no residual trees from before the fire. In this region of 161 Siberia, there is little infilling after the initial post-fire establishment period because changes in 162 the seedbed and competition from non-trees reduces germination opportunities (Matveeva and 163 Matveev 2008). In addition, there is little self-thinning in the high- and very-high-density stands, 164 as indicated by little woody debris and few standing dead trees that are not charred (Alexander et 165 al. 2012). There have been no ground fires in the study area since the original 1940 fire that 166 would have affected subsequent tree density. Further, surveys of charred coarse woody debris, 167 standing dead, and live residual trees within the fire perimeter indicate that there was no density 168 gradient in pre-fire stands, which were likely homogeneous with a low density (< 3,000169 stems/ha) of large larch (> 20 cm diameter at breast height (dbh)) trees. 170 Using satellite imagery and field reconnaissance, we identified 25 stands (Figure 1) 171 within the fire perimeter that varied in overstory tree density. We were specifically interested in 172 variation in tree density, rather than basal area, because density is an indicator of post-fire 173 recruitment in boreal forests (Alexander 2018; Johnstone et al. 2004). In 2016 and 2017, we

174 sampled three plots within each of the 25 stands for understory plant composition, forest stand 175 structure, and environmental conditions. All stands occurred in upland areas with no discernible 176 variation in drainage characteristics or topography, and there was little variation in elevation 177 across stands (range 23 - 93 m above sea level). Within each stand, plots were at least 30 m apart 178 and consisted of a variable-width, 30-m length belt transect. To ensure that we sampled a 179 representative number of trees in any given plot, the width of the belt transect ranged from 1 m 180 wide in the stands with the highest tree density to 8 m wide in the stands with the lowest tree 181 density (30-240 m<sup>2</sup>).

## 182 Stand Structure and Environmental Conditions

183 To measure stand structure, we surveyed all live and dead Cajander larch trees within 184 each belt transect by measuring the dbh of trees  $\geq 1.4$  m tall, and basal diameter (bd) of trees  $\leq$ 185 1.4 m tall. We calculated larch tree density as the number of all live larch trees, regardless of 186 height, per survey area (trees/m<sup>2</sup>), and live larch basal area as the total basal area per m<sup>2</sup> ( *basal area* =  $\pi (dbh/2)^2$ ), similar to Walker et al. (*In Press*). One high-density stand was 187 188 sampled in 2010 as part of another study (Alexander et al. 2012), when a series of five 1 x 20-m 189 belt transects were used to sample trees. Because those plots do not correspond directly with the 190 three plots used to sample other environmental variables in this current study, we calculated the mean tree density and basal area per m<sup>2</sup> across all five 2010 plots and assigned these mean 191 192 values to the tree density and basal area for each plot in that stand for this study. For data 193 visualization/interpretation we used a categorization of the density gradient (e.g., Figure 2, Table 194 1), where we split the plots into four approximately equal tree density categories: low (< 3,500195 stems/ha), medium (  $\geq$  3,500 and < 10,000 stems/ha), high (  $\geq$  10,000 and < 20,000 stems/ha), 196 and very high (  $\geq 20,000$  stems/ha).

We used a convex spherical densiometer to estimate canopy cover and characterize the amount of light available in the forest understory (Englund et al. 2000). In most plots, we took four densiometer readings corresponding to the cardinal directions at 0, 15, and 30 m along the center of the belt transect (12 total). In two stands, we collected densiometer readings at 0, 5, 10, 15, and 20 m along the belt transect (20 total). We calculated the mean of all measurements in a given plot to determine mean canopy cover for each plot.

203 In September 2017, we estimated active layer depth every 5 m along the center of each 204 belt transect using a metal thaw probe. At each location, the thaw probe was pushed into the soil 205 until the layer of frozen soil was reached, and the active layer depth was calculated as the 206 distance between the bottom of the green moss or lichen layer to the tip of the thaw probe. We 207 estimated SOL depth by cutting into the SOL adjacent to each understory quadrat with a serrated 208 knife and measuring the thickness of the litter, green moss or lichen, brown moss, fibric, and 209 humic layers. We considered SOL depth to be the sum of the litter, brown moss, fibric, and 210 humic components of the SOL profile.

211 Survey of Understory Vegetation

212 Between 2016 and 2017, we assessed plant community composition in each plot using 213 the point-intercept method in a series of quadrats located at the 5-m mark of each belt transect (1 214 quadrat per plot, 3 plots per stand, 75 quadrats total). The 0.25-m<sup>2</sup> quadrat was divided into 25 215 10 x 10-cm grid cells, and we placed a pin flag (0.3 cm diameter) through each of the 25 grid 216 intersection points. At each intersection point, we counted the number of times each plant 217 touched the pin flag. We identified each plant to the genus- or species- level and grouped all 218 grasses and sedges into a single graminoid category. The point-intercept method provides an 219 efficient estimate of total biomass of different species and cover types in a plot (Mamet et al.

220 2016). While this method may overlook rare species, it is sufficient for detecting general trends 221 across a plant community (Mamet et al. 2016). For this study, we were interested in species 222 abundance, composition, and diversity, rather than biomass. Therefore, we summed the number 223 of unique times that a given species intersected the grid across the 25 grid-intercept points in 224 each quadrat. For instance, if a species touched the pin flag twice at a given intersection point, 225 we counted this as a single intersection. Thus, there was a maximum of 25 possible grid-226 intersection points for each species in each quadrat. This measure can be considered an estimate 227 of percent cover for each species, and will be referred to as species abundance throughout the 228 paper.

We also used the point-intercept vegetation surveys to estimate the amount of larch, shrub, and grass litter in each quadrat. We noted when each litter type touched the pin flag and summed the number of intersections across all intersection points in the quadrat. In this case, because we were trying to estimate the relative biomass of each type of litter, we summed all intersections at each intersection point, meaning that there could be > 25 intersections across the 25 intersection points.

### 235 Statistical Analysis

Data used in this study are available at the Arctic Data Center (Alexander 2018), and analyses were conducted using R version 3.6.0. We used a combination of linear mixed models, ordination, and multilevel models to test our hypotheses. To avoid multicollinearity in the regression models, we calculated the Pearson correlation coefficient for each pair of environmental variables, and chose a set of three environmental variables to represent the environmental conditions across the density gradient: canopy cover, active layer depth, and SOL depth. 243 We used linear mixed models to compare the proportion of point-intercept hits from each 244 plant functional group in the 75 quadrats across the density gradient, using stand as a random 245 effect to account for the study design with three quadrats in each of the 25 stands. To do so, we 246 assigned each plant species to the following categories (Table S1): tall shrubs (with growth 247 forms > 1 m height), short shrubs (with growth forms < 1 m height), herbs, mosses, lichens, and 248 graminoids (grasses and sedges). We checked model residuals for both normality and 249 homogeneity of variance and used a square root transformation to improve adherence to model 250 assumptions where necessary.

251 We then tested the relationship between species diversity and environmental conditions 252 in our plots. We calculated species diversity using Hill numbers  $(^{q}D)$ , which provide a unifying 253 framework for understanding species richness and evenness and obey the doubling property of 254 pooled assemblages that many other diversity metrics fail to pass (reviewed in Chao et al. 2014). Hill numbers provide estimates of the effective number of species in a community, or the number 255 256 of equally abundant species needed to produce a given diversity estimate (Chao et al. 2014). In 257 the Hill number framework, the emphasis placed on rare species declines as the value of q 258 increases. We used Hill numbers of q = 0, 1, and 2 (equivalent to species richness, the exponent 259 of Shannon's entropy, and the inverse Gini-Simpson index, respectively), where species richness 260 is independent of species abundance and the inverse Gini-Simpson index weights abundant 261 species more heavily than rare species. We regressed each diversity metric versus environmental 262 conditions using linear mixed models with three centered and scaled (mean = 0, variance = 1) 263 environmental predictors: canopy cover, active layer depth, and SOL thickness, with stand as a 264 random effect to account for the sampling design. We confirmed that model assumptions were 265 met by assessing patterns of residuals versus fitted values and each predictor variable and

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confirmed that the distribution of residuals was approximately normal. Diversity values were
calculated using the vegan package (Oksanen et al. 2019) and linear mixed models were
developed using the lme4 package (Bates et al. 2015). We calculated p-values for fixed effects
using the Satterthwaite approximation in package lmerTest (Kuznetsova et al. 2017) and
calculated conditional and marginal model R<sup>2</sup> values using the piecewiseSEM package
(Lefcheck 2016).

272 We used non-metric multidimensional scaling (NMDS) ordination to visualize changes in 273 understory plant community composition across the tree density gradient. We used a Wisconsin 274 double standardization to standardize abundance values in our stand x species matrix (Bray and 275 Curtis 1957). We then used the Bray-Curtis distance metric to calculate dissimilarity in species' 276 composition across all quadrats (Bray and Curtis 1957). We used three axes with a maximum of 277 100 random starts for the NMDS ordination. We fit vectors to the ordination that showed the 278 relationship between all environmental variables and species composition in ordination space. To 279 do so, we used 999 permutations of the environmental data to determine the significance of each 280 environmental variable. We also plotted species scores in ordination space to approximate where 281 species and species groups had the highest abundance. We used the vegan package (Oksanen et 282 al. 2019) for all ordination analyses.

Lastly, we used multilevel models (MLM, Jackson et al. 2012) to assess changes in community- and species-level composition in stands with different environmental conditions. MLM provide an advantage over standard multivariate methods (e.g., NMDS, redundancy analysis) because they allow users to detect environmental drivers that affect all species as well as environmental drivers that affect species in different ways (Jackson et al. 2012). Further, MLM has higher statistical power than standard multivariate techniques to distinguish between 289 the effects of different environmental variables (Jackson et al. 2012). MLM analyses include 290 both fixed effects that predict the abundance of all species across environmental gradients, and 291 random effects that account for the variation in different species' responses to environmental 292 gradients. Using the lme4 package (Bates et al. 2014), we fit a MLM with a binomial response 293 (total number of intersections of a given species out of 25 possible intersections in each quadrat) 294 with stand included as a random effect. We also included species as a random effect and allowed 295 both slopes and intercepts to vary for each species as a response to three centered and scaled 296 environmental predictors: canopy cover, SOL depth, and active layer depth. Because the initial 297 binomial model showed strong evidence of overdispersion, we included an observation-level 298 random effect, converting the model to a binomial normal model (Browne et al. 2005). We used 299 likelihood ratio tests to assess the significance of random effect slopes for each environmental 300 predictor and Wald Z-tests to assess the significance of fixed effects. We did not test the 301 significance of stand and species random effect intercepts, as these were part of the experimental 302 design. Marginal and conditional R<sup>2</sup> values were calculated as in the diversity analyses. To 303 estimate the effect of different environmental predictor variables on the abundance of each 304 species, we calculated the model coefficients for each species by summing the mean fixed effect 305 and random species slopes together. Following Romme et al. (2016), we considered species 306 coefficients > |0.20| to be evidence of a strong effect of an environmental variable on a given 307 species.

#### 308 Results

Across the study area, both tree density and basal area were positively correlated with canopy cover, negatively correlated with active layer depth, and not well correlated with SOL depth (Table 1). Canopy cover was also correlated with several other stand characteristics: 312

canopy cover was highest in stands with more fine woody debris (r = 0.44), more larch litter (r =

313	0.56), less shrub litter (r = -0.56), and shallower active layer depth (r = -0.53).
314	We observed a total of 27 understory species, genera, and species groups across the tree
315	density gradient (Table S1). The most common species were Vaccinium vitis-idaea and
316	Aulacomnium palustre (in 71 and 67 out of 75 quadrats, respectively). The proportional
317	abundance of graminoids (mean = $0.09$ ), herbs (mean = $0.08$ ), lichens (mean = $0.05$ ), and short
318	shrubs (mean = 0.30) did not vary significantly across the tree density gradient (Figure 3). The
319	proportional abundance of mosses was higher in stands with higher canopy cover (Figure 3D, p $\!<\!$
320	0.001, $R^2 = 0.495$ ). In contrast, the proportional abundance of tall shrubs increased in stands with
321	lower canopy cover (Figure 3F, $p = 0.002$ , $R^2 = 0.541$ ). A 25% absolute increase in canopy cover
322	was associated with an increase in proportional moss abundance by 0.08, and a decrease in
323	proportional tall shrub abundance by 0.06.

324 Understory plant diversity decreased with increasing canopy cover. Quadrat-level species 325 richness ranged from 3 to 15 species, with the highest richness in the low-density stands. Each 326 species diversity metric decreased with increased canopy cover (Table 2, Figure 4, p < 0.05 for each model), with no detected effects of active layer or SOL depth (p > 0.1). The modelled 327 328 effect size of the relationship between canopy cover and species diversity decreased with 329 increasing Hill numbers (Table 2), e.g., an increasing emphasis on common species (Chao et al. 330 2014). With a 25% absolute increase in canopy cover, the effective number of species decreased 331 by 0.73, 0.58, and 0.52 for Hill numbers 0, 1, and 2, respectively.

Ordination analyses demonstrated that a pronounced gradient in understory plant
 community composition occurred along the tree density gradient and that differences in
 community composition were correlated with multiple stand characteristics. NMDS ordination

335 showed differentiation between plant communities across the first NMDS axis (Figure 5, stress = 336 0.187). There was little overlap between low- and very-high-density quadrats, with low-density 337 quadrats clustered in the positive portion of the first NMDS axis and very-high-density quadrats 338 clustered in the negative portion of the first NMDS axis. High-density quadrats overlapped with 339 the very-high-density quadrats but were more spread out. Medium-density quadrats overlapped 340 with quadrats from all other tree density categories but grouped toward the center of the 341 ordination. The first NMDS axis was negatively correlated with stand characteristics like tree 342 density, larch litter, canopy cover, larch basal area, and fine woody debris, and positively 343 correlated with shrub litter and active layer depth (Figure 5A, Table S2). The tall shrub Betula 344 nana subsp. exilis, short shrubs Empetrum nigrum L. and V. uliginosum, and lichen Peltigera apthosa were most abundant towards the positive end of the first NMDS axis, associated with 345 346 quadrats from low-density stands (Figure 5B). In contrast, the short shrub V. vitis-idaea and 347 mosses like Sanionia spp. Loeske and A. palustre were more abundant in the negative portion of 348 the first NMDS axis, associated with high- and very-high-density stands. 349 Multilevel models (MLM) indicated that mean total plant abundance, independent of 350 species identity, decreased with increasing canopy cover and that canopy cover was the most 351 important variable affecting individual species' abundances. Canopy cover was the only fixed 352 effect with a strong relationship to mean total plant abundance, where a single standard deviation 353 increase in canopy cover (absolute increase of 25%) was associated with a 28% decrease in total 354 plant abundance (p = 0.009, Table 3) when all other variables were at their mean value. The 355 abundance of individual species was strongly associated with canopy cover (random slope effect, 356 p < 0.001), weakly with active layer depth (p = 0.108), and there was no evidence of a 357 relationship between SOL depth and species abundance (p = 0.246). Of the 27 species and

358 species groups identified in our plots, 18 of 27 (67%) had a strong response to canopy cover 359 (Table 4). For instance, the probability of observing *B. nana* subsp. *exilis* decreased with 360 increased canopy cover (Figure 6, coefficient = -0.910), while the genus *Sanionia* spp. was more 361 abundant in stands with higher canopy cover (coefficient = 0.291). Three species and species 362 groups (11%) were associated with changes in active layer depth (Table 4). E. nigrum and Salix 363 spp. were more abundant in stands with deeper active layer depths (coefficients = 0.282 and 364 0.267, respectively), while A. palustre was less abundant in stands with deeper active layer 365 depths (Figure 6, coefficient = -0.289). No species' responses were associated with SOL depth (Table 4). 366

## 367 Discussion

368 Understory plant communities in Cajander larch stands with different tree densities 369 varied in species diversity, abundance, and composition. Species diversity and the abundance of 370 most species decreased with increasing canopy cover. Understory plant species composition 371 varied across the tree density gradient and was strongly associated with variation in canopy 372 cover. Tall shrubs were more abundant in low-density stands while mosses were more abundant 373 in higher-density stands. These results indicate that initial differences in post-fire larch 374 recruitment can have long-lasting consequences for and interactions with understory plant 375 communities as stands mature. This is important because changes in the abundance of understory 376 vegetation from different functional types can influence ecosystem processes. 377 As hypothesized, understory plant species richness and diversity decreased with 378 increasing larch canopy cover, with as few as three species in some quadrats from very-high-379 density stands. These patterns are likely due to increased resource availability in low-density

380 forests (Bartels and Chen 2010). Lower-density larch forests have increased light availability and

381 are associated with higher diversity and a higher abundance of vascular, lichen, and bryophyte 382 species. In contrast, high-density larch forests have reduced availability of light, nutrients, and 383 space (De Grandpré et al. 1993; Hart and Chen 2006) and have the lowest diversity. These 384 patterns reflect observations from Dahurian larch forests, where low-density stands with 385 increased solar radiation have the highest species richness (Ma et al. 2016) and higher lichen and 386 herbaceous cover than closed-canopy stands (Kobak et al. 1996). Additionally, the six least 387 abundant species in our study (e.g., forbs like Pedicularis labradorica Wirsing and Petasites 388 *frigidus*) were only identified in low- or medium-density stands, while most other species were 389 present with varying abundance across the density gradient. This matches findings in other 390 studies, where reduced diversity in closed-canopy forests was due to the loss of species (particularly forbs) from the community rather than a complete turnover in species composition 391 392 (e.g., De Grandpré et al. 1993). While we did not directly assess effects of resource heterogeneity 393 on species diversity, there could potentially be increased heterogeneity in lower-density forests 394 where there is a mix of both open and shaded environments and potentially increased 395 microtopographic variation due to increased active layer depths and more extreme variation in 396 freeze-thaw cycles (Zyryanova et al. 2007). The decrease in plant species diversity with 397 increased canopy cover indicates that changes in tree density following fires can influence long-398 term patterns of understory plant diversity. In areas where lower-density forests develop, we may 399 see long-term increases in understory plant diversity, particularly of shrubs and shade-intolerant 400 forbs. 401 We found evidence that differentiation in understory plant community composition

402 across the tree density gradient was strongly related to stand characteristics and abiotic

403 conditions. The abundance of most species was lower in stands with higher canopy cover, likely

404 due to reduced resource availability in closed-canopy forests (Hart and Chen 2006). In contrast, 405 the abundance of the feather moss genus, Sanionia spp., was highest in stands with higher 406 canopy cover. This result is similar to that observed in North American black spruce (Picea 407 mariana (Mill.) Britton, Sterns & Poggenb.) forests, where feather mosses were more abundant 408 in late-successional, closed-canopy forests compared to early-successional, open-canopied 409 forests (Jean et al. 2017). Even though active layer depth was not associated with overall species 410 abundance, deeper active layer depths were positively associated with two shrub species 411 (Empetrum nigrum and Salix spp.), and negatively associated with the moss Aulacomnium 412 *palustre*. In boreal forests, shrubs tend to thrive in areas with increased light availability, and 413 deeper active layers with increased nutrient availability (Wookey et al. 2009; Hart and Chen 414 2006; Schuur et al. 2007). In the larch forests of this study, stands with the lowest canopy cover 415 had warmer soils (mean 0.9 °C versus -2.8 °C in very-high-density stands) and deeper active 416 layers. When these conditions occur in the tundra due to thermokarsting or warming 417 experiments, decomposition rates and inorganic nitrogen availability increase (Salmon et al. 418 2016), favoring increased shrub cover (Schuur et al. 2007). Thus, the increase in shrub cover that 419 we observed in low density stands may be due, in part, to increased decomposition rates and 420 nutrient availability in warmer soils with deeper active layers. In contrast with other boreal forest 421 understories (De Grandpré et al. 1993; Jean et al. 2017), we did not find evidence of a 422 relationship between SOL depth and understory plant species abundance in these larch stands. 423 Stand characteristics, abiotic conditions, and understory plant community composition 424 are tightly linked in these forests, which complicates our ability to identify causation for the 425 observed patterns. For instance, tree density and canopy cover were strongly correlated with 426 variation in leaf litter types, woody debris, and other abiotic conditions in our study, and these

427 characteristics can then impact microsite heterogeneity, soil pH, and nutrient availability (Hart 428 and Chen 2006). Consequently, which of these variables or combinations of variables are the 429 primary drivers of understory plant community composition is unclear. Further, abiotic 430 conditions like active layer depth are strongly correlated with vegetation cover (Loranty et al. 431 2018), but we cannot determine whether active layer depth drives community composition or 432 vice-versa. Despite these caveats, we still identified strong differentiation in diversity and 433 composition of plant communities across the tree density gradient, which may have a strong 434 impact on ecosystem function.

435 The shift from tall shrub to moss dominance in low-versus high-density forests can have 436 ecosystem-level consequences. For instance, in areas with high shrub abundance, the 437 accumulation of snow around tall shrubs can insulate the soil from cold winter temperatures and 438 lead to increased soil temperatures during the winter and early spring (Wookey et al. 2009). 439 Warmer soils allow microbial activity to occur throughout the year, thereby increasing nitrogen 440 mineralization rates, and promoting further increases in shrub abundance (Wookey et al. 2009). 441 Variation in shrub composition can also impact nutrient cycling and decomposition rates 442 (DeMarco et al. 2014). For example, litter from *Vaccinium vitis-idaea* decomposes more quickly 443 and has higher nitrogen mineralization rates than *E. nigrum* (Nilsson and Wardle 2005). 444 Additionally, even though the amount of carbon stored in understory plants is higher in low-445 versus high-density forests, it is insufficient to offset the increases in carbon stored in trees in 446 higher-density forests; thus, low-density forests with increased shrub cover have lower total 447 aboveground carbon storage compared with higher-density forests (Sigurdsson et al. 2005; 448 Alexander et al. 2012). Lastly, shrubs can act as an additional filter (beyond seed source 449 availability, abiotic conditions, etc.) to reduce tree establishment during early succession. Shrub

450 rhizomes buried deep within the SOL can survive high severity fires and initiate new aerial stems 451 immediately after fire (Uemura et al. 1990). These shrubs can then out-compete new tree 452 regeneration and other understory species by creating shady microclimates in which other 453 species are unable to persist (Hart and Chen 2006). Ericaceous shrubs (e.g., V. uliginosum and 454 *Rhododendron tomentosum*) may also reduce successful tree establishment via allelopathic 455 chemicals (Nilsson and Wardle 2005). Reduced tree regeneration due to competition from shrubs 456 might then lead to low-density forests with higher winter-time albedo than high-density forests 457 (Loranty et al. 2014). In sum, variation in shrub composition across the density gradient likely 458 has strong ecosystem effects via changes in carbon storage, nutrient cycling, albedo, and tree 459 recruitment.

460 Mosses, which were more common in the closed-canopy, higher-density stands, can also 461 have a strong effect on ecosystem processes. Because mosses are often moisture-limited 462 (Turetsky et al. 2012), moss diversity tends to increase with post-fire canopy cover in boreal 463 forests as conditions become cooler and moister (Hart and Chen 2006). While some moss species 464 are nitrogen fixers, many mosses decompose slowly and immobilize nutrients from soils 465 (Nilsson and Wardle 2005; Turetsky et al. 2012). Thus, the increase in feather moss abundance 466 with canopy closure could negatively affect tree regeneration by restricting seedling access to 467 nutrients (Nilsson and Wardle 2005). Additionally, evidence from Northern Sweden suggests 468 that, relative to their biomass, mosses contribute disproportionately to above ground net primary 469 productivity during early spring and late summer when trees are no longer photosynthesizing 470 (Campioli et al. 2009). Mosses also play an important role in the development of the SOL in 471 boreal forests, where cool temperatures and slow decomposition rates lead to the accumulation of 472 organic matter (Turetsky et al. 2012). Areas with a deeper SOL and more moss accumulation

473 tend to have cooler soil temperatures and shallower active layer depths (Sofronov and Volokitina 474 2010; Turetsky et al. 2012; Loranty et al. 2018), protecting permafrost from warmer air 475 temperatures during the growing season (Turetsky et al. 2012). In our study, the interaction 476 between increased moss cover and shading from trees likely played a role in cooler soils and 477 shallower active layers, which may promote permafrost stability in these higher-density forests. 478 Our study provides evidence that differences in post-fire forest composition and structure 479 affect understory plant species diversity and composition in the Cajander larch forests of 480 northeast Siberia. Ongoing increases in fire activity (Shvidenko and Schepaschenko 2013; 481 Ponomarev et al. 2016) that affect forest structure and composition will likely lead to changes in 482 the understory plant community. Stands with low post-fire seed source availability (Cai et al. 483 2013) or poor conditions for larch establishment (Sofronov and Volokitina 2010; Cai et al. 2013; 484 Alexander et al. 2018) may develop with low tree density. In this study, stands with low 485 Cajander larch density had higher understory plant species diversity, higher shrub abundance, 486 and lower moss abundance compared to stands with high tree density. These changes in 487 understory composition interact with forest composition and structure and can influence 488 ecosystem processes by changing albedo, carbon storage, and net primary productivity. This 489 study provides a snapshot of tree and understory dynamics within a 76-year-old fire perimeter 490 and highlights that tree demographic patterns are strongly linked with understory plant dynamics.

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490 Competing micresis	496	<b>Competing interests</b>
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497 The authors declare there are no competing interests.

## 498 Author Contributions

- 499 Conceptualization: AKP, HP, HDA, MCM; Methodology: AKP, HP, HDA, MCM;
- 500 Software and formal analysis: AKP; Validation: AKP, HP, HDA, SPD, MCM; Investigation:
- 501 HP, HDA, SPD, MML, MCM, SMN; Resources: HDA, SPD, MCM; Data curation: AKP, HP,
- 502 HDA; Writing original draft: AKP; Writing review and editing: all authors; Visualization:
- 503 AKP; Supervision: HDA, MCM; Project administration: AKP, HP, HDA, MCM; Funding
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## 509 Data Availability

- 510 Data used in this study are archived and available at the National Science Foundation
- 511 Arctic Data Center (PID: doi:10.18739/A2736M18D, https://doi.org/10.18739/A2736M18D).

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# 683 Tables

Table 1: Total count (N) and mean stand characteristics for Cajander larch stands across a postfire tree density gradient in northeast Siberia: low (< 3,500 stems/ha), medium ( $\geq$  3,500 and < 10,000 stems/ha), high ( $\geq$  10,000 and < 20,000 stems/ha), and very high ( $\geq$  20,000 stems/ha). The last two columns, r(Dens) and r(BA), show the Pearson correlation coefficient of each stand characteristic with tree density and basal area, respectively (correlations with p-values  $\leq$  0.05 are bolded).

Characteristic	Low	Medium	High	Very High	r(Dens)	r(BA)
Ν	5	8	6	6		
Tree Density (stems/ha)	878 ± 197	5,573 ± 607	14,690 ± 1,371	28,093 ± 2,502		0.55
Basal Area (m²/ha)	2.4 ± 0.8	10.5 ± 1.4	20.4 ± 1.3	15.2 ± 1.2	0.55	
Canopy Cover (%)	13.6 ± 4.0	41.4 ± 4.6	70.2 ± 6.3	62.4 ± 4.2	0.68	0.85
Active Layer Depth (cm)	78.2 ± 7.2	52.0 ± 2.9	49.8 ± 3.6	50.1 ± 1.4	-0.45	-0.60
SOL Depth (cm)	8.8 ± 1.2	10.7 ± 0.8	9.6 ± 1.0	9.7 ± 0.5	-0.04	0.01

690

692	Table 2: Estimated linear mixed model effects of canopy cover (%), active layer depth (cm), and
693	soil organic layer depth (cm) on species diversity of understory vegetation (p-values $< 0.05$ are
694	bolded) across a post-fire Cajander larch tree density gradient in northeast Siberia. Predictor
695	variables were centered and scaled (mean = $0$ and variance = $1$ ), making the model coefficients
696	directly comparable within each model. Forest stand was included as a random effect in the
697	model to account for the three quadrats surveyed within each stand.

	Species Ri	chness (H	lill = 1)	Exponent Entrop	tial Shanı by (Hill =	non's 2)	Inverse Si	mpson (H	lill = 3)
Fixed Effects	Estimate	t	р	Estimate	t	р	Estimate	t	р
Intercept	7.51 ± 0.32	23.69	< 0.001	5.36 ± 0.2	26.31	< 0.001	4.44 ± 0.16	27.75	< 0.001
Canopy Cover	-0.73 ± 0.35	-2.10	0.042	-0.58 ± 0.22	-2.61	0.012	-0.52 ± 0.18	-2.94	0.005
Active Layer	0.22 ± 0.35	0.63	0.535	0.26 ± 0.23	1.15	0.256	0.21 ± 0.18	1.17	0.247
Soil Organic Layer	-0.03 ± 0.25	-0.12	0.902	0.11 ± 0.16	0.70	0.485	0.22 ± 0.13	1.64	0.106
Marginal R <sup>2</sup>	0.133			0.215			0.254		
Conditional R <sup>2</sup>	0.366			0.422			0.429		

698

700	Table 3: Estimated multilevel model fixed and random effects of canopy cover (%), active layer
701	depth (cm), and soil organic layer depth (cm) on understory species abundance (p-values < 0.05
702	are bolded) across a post-fire Cajander larch tree density gradient in northeast Siberia. Predictor
703	variables were centered and scaled (mean = 0 and variance = 1), and forest stand was included as
704	a random effect in the model to account for the three quadrats surveyed within each of 25 stands.
705	Species (Intercept) indicates the variance associated with individual species' abundances, e.g.,
706	the random intercept parameter. Species (Canopy Cover), Species (Active Layer), and Species
707	(Soil Organic Layer) indicate the variance associated with individual species' responses to stand
708	characteristics, e.g., the random slope parameters.

Fixed Effects	Estimate	z-value	p-value
Intercept	-5.63 ± 0.46	-12.13	< 0.001
Canopy Cover	-0.33 ± 0.13	-2.60	0.009
Active Layer	$0.04 \pm 0.11$	0.34	0.737
Soil Organic Layer	$-0.02 \pm 0.08$	-0.25	0.802
Marginal R <sup>2</sup>	0.006		
Conditional R <sup>2</sup>	0.449		
Random Effects	Variance	p-value	
Species (Intercept)	5.59		
Species (Canopy Cover)	0.18	< 0.001	
Species (Active Layer)	0.07	0.108	
Species (Soil Organic Layer)	0.04	0.246	
Stand (Intercept)	0.10		
Obs (Intercept)	3.12		

709

- 711 Table 4: Multilevel model coefficients for understory plant species abundance responses to
- canopy cover (%), active layer depth (cm), and soil organic layer depth (cm) 76 years post-fire
- along a Cajander larch tree density gradient in northeast Siberia.

Species <sup>a</sup>	Canopy Cover <sup>b</sup>	Active Layer <sup>b</sup>	Soil Organic Layer <sup>b</sup>
<i>Betula nana</i> subsp. <i>exilis</i>	-0.910	0.078	0.199
Peltigera aphthosa	-0.633	0.013	0.006
Vaccinium uliginosum	-0.622	0.175	0.031
<i>Cladonia</i> spp.	-0.556	0.076	-0.030
Petasites frigidus	-0.552	0.110	-0.065
Rosa acicularis	-0.551	0.076	-0.083
Pedicularis labradorica	-0.474	0.032	-0.086
Tomentypnum nitens	-0.464	0.135	-0.004
Flavocetraria cucullata	-0.462	0.199	-0.053
Unknown Moss	-0.460	0.041	-0.039
Cetraria islandica	-0.427	0.032	-0.067
Arctous alpina	-0.371	0.125	-0.078
Equisetum arvense	-0.362	0.076	-0.083
Rhododendron tomentosum	-0.304	-0.039	-0.014
Empetrum nigrum	-0.288	0.282	0.052
Dicranum spp.	-0.267	0.070	-0.013
Graminoid	-0.220	-0.057	-0.071
<i>Salix</i> spp.	-0.188	0.267	-0.001
Equisetum scirpoides	-0.161	-0.080	0.161
Peltigera neopolydactyla	-0.134	-0.124	-0.065
Polytrichum spp.	-0.105	0.016	-0.070
Valeriana capitata	-0.089	-0.022	-0.043
Vaccinium vitis-idaea	-0.081	-0.056	0.089
Ptilidium ciliare	-0.037	-0.089	0.089
Aulacomnium palustre	-0.010	-0.289	-0.035

Species <sup>a</sup>	Canopy Cover <sup>b</sup>	Active Layer <sup>b</sup>	Soil Organic Layer <sup>b</sup>
<i>Pyrola asarifolia</i> subsp. <i>asarifolia</i>	0.113	-0.082	-0.061
<i>Sanionia</i> spp.	0.291	-0.103	-0.174

<sup>a</sup>Species are ordered by the strongest negative to the strongest positive response to canopy cover. Some species were only identified to the genus-level in the field. All sedges and grasses were grouped into a single graminoid category. Additional taxonomic information and functional group classification is available in Table S1.

<sup>b</sup>Coefficients are the sum of the estimates for the fixed (mean slope) and random effects (species-level variation in slope) for each species and stand characteristic. Coefficients > [0.20] are bolded to indicate a strong effect of a stand characteristic on species abundance. Negative values indicate a negative relationship between the stand characteristic and species abundance; positive values indicate a positive relationship. Predictor variables were centered and scaled (mean = 0 and variance = 1), making the model coefficients directly comparable.

## 714 Figure Captions

- Figure 1: Study area near the Northeast Science Station in Cherskiy, Russia (orange star; 68.76 °
- N, 161.46 °E): A) Study area in northeast Siberia; B) Sampling locations from panel C are
- 717 highlighted by a black box and shown in reference to the Kolyma River and the Northeast
- Science Station; C) Specific locations of each of the low (< 3,500 stems/ha), medium (  $\geq$  3,500
- 719 and < 10,000 stems/ha), high ( $\geq$  10,000 and < 20,000 stems/ha), and very high ( $\geq$  20,000
- stems/ha) Cajander larch stands within a fire perimeter that burned in 1940. Panel A was
- produced using the R package oce (Kelley and Richards 2020) and the 'coastlineWorldMedium'
- base map. Panels B (WorldView 2 Multispectral Imagery from 11 July 2011 provided by the
- 723 Polar Geospatial Center) and C (WorldView2 Panchromatic Imagery from 8 March 2015
- provided by the Polar Geospatial Center) were produced using ArcMap 10.8.1.
- 725

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726	Figure 2: Overstory (left) and understory (right) photos of forest stands along the Cajander larch
727	tree density gradient in northeast Siberia, with low (A and B; < 3,500 stems/ha), medium (C and
728	D; $\geq$ 3,500 and < 10,000 stems/ha), high (E and F; $\geq$ 10,000 and < 20,000 stems/ha), and very
729	high (G and H; $\geq$ 20,000 stems/ha) tree density. Panels A) and B) show a high abundance of the
730	tall shrub Betula nana subsp. exilis in the understory, whereas mosses like Sanionia spp. or
731	Aulacomnium palustre are more abundant in the higher-density forest understories shown in
732	panels F) and H).
733	
734	Figure 3: Relative proportion of different understory plant species functional groups across the
735	post-fire Cajander larch tree density gradient in northeast Siberia. Solid lines indicate a
736	significant effect (p < $0.002$ ) of tree density on a given functional group, while dotted lines
737	indicate no observed effect of tree density ( $p > 0.2$ in all cases). Points represent the mean
738	observed proportion of each functional group within each stand (25 stands, 3 quadrats per stand);
739	stand was included as a random effect in the model.
740	
741	Figure 4: Effective number of understory plant species across a post-fire Cajander larch tree
742	density gradient in northeast Siberia plotted as a function of canopy cover when active layer
743	depth and soil organic layer depth are at their mean values: A) species richness, B) exponential
744	Shannon's entropy, and C) the inverse Simpson metric. Points represent the mean observed
745	effective number of species within each stand (25 stands, 3 quadrats per stand); stand was
746	included as a random effect in the model.
747	
748	Figure 5: NMDS ordination of understory plant species composition for all quadrats across the

post-fire Cajander larch tree density gradient in northeast Siberia (stress = 0.187). Quadrats are

- 750coded by shape and color to represent their position along the tree density gradient: low (< 3,500</th>751stems/ha), medium ( $\geq$  3,500 and < 10,000 stems/ha), high ( $\geq$  10,000 and < 20,000 stems/ha),</td>752and very high ( $\geq$  20,000 stems/ha). We included A) environmental vectors representing the753relationship between stand characteristics and species composition in different quadrats, and B)754species scores for the 10 most abundant species and species groups representing the weighted755average of species abundance in ordination space.756Figure 6: Multilevel model predictions and 95% confidence intervals for understory plant species
- abundance (% of intersections in a quadrat) in response to percent canopy cover for A) *Betula*
- nana subsp. exilis and B) Sanionia spp., and in response to active layer depth for C)
- 760 *Aulacomnium palustre* and D) *Salix* spp. across the post-fire Cajander larch tree density gradient
- 761 in northeast Siberia.

763

## 762 Figures



764 Figure 1: Study area near the Northeast Science Station in Cherskiy, Russia (orange star; 68.76 ° 765 N, 161.46 °E): A) Study area in northeast Siberia; B) Sampling locations from panel C are 766 highlighted by a black box and shown in reference to the Kolyma River and the Northeast 767 Science Station; C) Specific locations of each of the low (< 3,500 stems/ha), medium (  $\geq$  3,500 768 and < 10,000 stems/ha), high ( $\geq 10,000$  and < 20,000 stems/ha), and very high ( $\geq 20,000$ 769 stems/ha) Cajander larch stands within a fire perimeter that burned in 1940. Panel A was 770 produced using the R package oce (Kelley and Richards 2020) and the 'coastlineWorldMedium' 771 base map. Panels B (WorldView 2 Multispectral Imagery from 11 July 2011 provided by the 772 Polar Geospatial Center) and C (WorldView2 Panchromatic Imagery from 8 March 2015 773 provided by the Polar Geospatial Center) were produced using ArcMap 10.8.1.



Figure 2: Overstory (left) and understory (right) photos of forest stands along the Cajander larch tree density gradient in northeast Siberia, with low (A and B; < 3,500 stems/ha), medium (C and D;  $\geq$  3,500 and < 10,000 stems/ha), high (E and F;  $\geq$  10,000 and < 20,000 stems/ha), and very high (G and H;  $\geq$  20,000 stems/ha) tree density. Panels A) and B) show a high abundance of the tall shrub *Betula nana* subsp. *exilis* in the understory, whereas mosses like *Sanionia* spp. or *Aulacomnium palustre* are more abundant in the higher-density forest understories shown in panels F) and H).



Figure 3: Relative proportion of different understory plant species functional groups across the post-fire Cajander larch tree density gradient in northeast Siberia. Solid lines indicate a significant effect (p < 0.002) of tree density on a given functional group, while dotted lines indicate no observed effect of tree density (p > 0.2 in all cases). Points represent the mean observed proportion of each functional group within each stand (25 stands, 3 quadrats per stand); stand was included as a random effect in the model.





Figure 4: Effective number of understory plant species across a post-fire Cajander larch tree density gradient in northeast Siberia plotted as a function of canopy cover when active layer depth and soil organic layer depth are at their mean values: A) species richness, B) exponential Shannon's entropy, and C) the inverse Simpson metric. Points represent the mean observed effective number of species within each stand (25 stands, 3 quadrats per stand); stand was included as a random effect in the model.

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Figure 5: NMDS ordination of understory plant species composition for all quadrats across the post-fire Cajander larch tree density gradient in northeast Siberia (stress = 0.187). Quadrats are coded by shape and color to represent their position along the tree density gradient: low (< 3,500 stems/ha), medium ( $\geq$  3,500 and < 10,000 stems/ha), high ( $\geq$  10,000 and < 20,000 stems/ha),

- and very high ( $\geq 20,000$  stems/ha). We included A) environmental vectors representing the
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- species scores for the 10 most abundant species and species groups representing the weighted
- 807 average of species abundance in ordination space.
- 808



810 Figure 6: Multilevel model predictions and 95% confidence intervals for understory plant species

811 abundance (% of intersections in a quadrat) in response to percent canopy cover for A) Betula

812 *nana* subsp. *exilis* and B) *Sanionia* spp., and in response to active layer depth for C)

813 Aulacomnium palustre and D) Salix spp. across the post-fire Cajander larch tree density gradient

814 in northeast Siberia.