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Species-specific trends and variability in plant functional traits across a latitudinal gradient in northern Alaska

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Abstract

Questions: Many studies explore how plant functional traits may change as the climate warms by observing traits over environmental gradients. The amount of intraspecific variation (ITV), however, is often unknown and unaccounted for in most trait-based studies. Our objectives are to: (a) determine if species-level patterns across a latitudinal gradient match those of other members within the same growth form; (b) compare distributions of trait values across regions; and (c) quantify the amount of ITV within each trait relative to the amount of variation within the growth form and across taxonomic levels (family and species).

Location: Utqiaġvik, Atqasuk, and Toolik Lake, Alaska.

Methods: This study examines seven plant functional traits for 12 arctic species. Traits were measured on 10 individuals of each species at each region and analyzed using one-way ANOVA and variance partitioning via nested ANOVA.

Results: Comparison of mean trait values across the three regions for each species showed considerable variability within a growth form. Within deciduous shrubs, for example, one species increased in specific leaf area (SLA) with latitude while another species decreased. Results from variance partitioning differed among functional traits. Across the three regions, plant height, leaf area, SLA, leaf thickness, and leaf dry matter content (LDMC) had relatively low amounts of intraspecific variation (ITV; <15%) while normalized difference vegetation index (NDVI) had a high amount of ITV (>50%). All traits showed significant differences across regions for at least some species.

Conclusions: Because our results showed considerable variability in levels of ITV among functional traits, we emphasize the need to investigate ITV in trait-based studies spanning multiple regions. Levels of ITV are important in determining how different populations respond to local environmental conditions. Incorporating ITV in studies investigating vegetation change with warming will provide more robust and reliable predictions.

KEYWORDS
arctic, growth form, International Tundra Experiment, intraspecific variation, tundra, variance partitioning

1 | INTRODUCTION

The rate of global climate change has been steadily increasing over the last several decades (IPCC, 2018). Climate change is occurring even faster in the northernmost latitudes, with temperatures increasing at twice the rate of the global average (ACIA, 2004; AMAP, 2019). The Arctic is also experiencing reduced snow cover and duration, increased thawing of the permafrost, and rapid declines in sea ice extent (AMAP, 2019). Observed changes are due to rapidly rising temperatures, making the Arctic an early indicator of future environmental change in other regions (McGuire et al., 2006). The Arctic is at the forefront of climate change impacts (AMAP, 2019; IPCC, 2018) and will likely continue to be for decades to come.

Plant communities have been shown to change with increased temperature (Walker et al., 2006; Elmendorf et al., 2012; Hollister et al., 2015; Edwards & Henry, 2016; Bjorkman et al., 2020). The Arctic is a harsh environment with cool summer temperatures, low nutrient availability, and a short growing season. Arctic plant species, therefore, fall under Grime's stress-tolerant life strategy (Grime, 1977) and are commonly short-statured evergreen shrubs and low-growing forbs along with bryophytes and lichens; in the lower Arctic, however, deciduous shrubs and graminoids are dominant (Walker et al., 2005). Documented change in community composition in association with decadal warming trends have consistently found increases in evergreen shrubs, deciduous shrubs, and graminoids and decreases in bryophytes and lichens (Callaghan et al., 2011; Elmendorf et al., 2012; Hollister et al., 2015; Bjorkman et al., 2020). Analysis by growth form (most often deciduous shrubs, evergreen shrubs, graminoids, forbs, bryophytes, and lichens) is commonly used because species within the same growth form often influence ecosystem dynamics in similar ways (Chapin et al., 1996). Growth form responses to increased temperature are not consistent at all sites, however, and analysis by growth form may mask species-specific responses. Species within growth forms exhibit a broad range of responses to environmental manipulations (Hudson et al., 2011; Saccone et al., 2017; Løkken et al., 2020), providing support for functional trait- and species-focused studies.

Many studies have also observed trends in functional traits along environmental gradients (Gao et al., 2018; Halbritter et al., 2018; de Villemereuil et al., 2018; Myers-Smith et al., 2019). In general, size-related traits such as plant height and leaf area decrease with increased latitude and elevation (i.e., temperature; Gao et al., 2018; Halbritter et al., 2018; de Villemereuil et al., 2018). Environmental gradient-based studies are often used as indicators for how functional traits will shift with climate warming since long-term data do not yet exist for many traits. Short-term simulated warming experiments using open-top chambers (OTCs) provide some evidence for temperature–trait relationships, but results are mixed (Hudson et al., 2011; Bjorkman et al., 2018a; Myers-Smith et al., 2019). Some species mirror results expressed by growth forms, but other species exhibit more individualistic responses. Differing responses of species within growth forms have been found within graminoids (Chapin & Shaver, 1985), deciduous shrubs (Chapin & Shaver, 1985; Press et al., 1998; Saccone et al., 2017), and evergreen shrubs (Chapin & Shaver, 1985; Press et al., 1998). Furthermore, temperature–trait relationships vary among species, making it difficult to understand each species-specific response to environmental changes.

Shifts in community composition along with shifts in plant functional traits with climate change can have important implications for ecosystem functioning. Functional traits such as plant height, specific leaf area (SLA), and leaf dry matter content (LDMC) strongly affect ecosystem processes such as primary productivity (Lavorel & Garnier, 2002; Díaz et al., 2004) and litter decomposability (Lavorel & Garnier, 2002; Santiago, 2007; Tao et al., 2019), and studies show increases in both plant height and SLA and decreases in LDMC with temperature (Hudson et al., 2011; Bjorkman et al., 2018a; de Villemereuil et al., 2018). SLA and LDMC are two traits that are part of the leaf economics spectrum, which takes the total amount of variation that exists within the plant kingdom and constrains it to a single axis describing plant form and function (Wright et al., 2004; Díaz et al., 2016). Other traits related to the leaf economics spectrum include leaf area and leaf thickness, which both influence how plants partition resources and therefore affect primary productivity (Wright et al., 2004; Osnas et al., 2013; Díaz et al., 2016). Water band index (WBI) and normalized difference vegetation index (NDVI) are also strong indicators of plant health and performance (Sellers, 1985; Camoglu & Genc, 2013). WBI has been used as a non-destructive method of estimating leaf water content (Peñuelas et al., 1993) which can be indicative of how plants respond to water stress (Claudio et al., 2006). Projections based on current community distributions predict that annual gross primary productivity (GPP) will increase by 31% in northern biomes (Madani et al., 2018). Increased GPP coupled with potential increases in litter and peat decomposition rates (indicated by increases in traits such as SLA and decreases in LDMC) may greatly alter the current carbon balance in the Arctic (McLaren et al., 2017; Parker et al., 2018). Changes in ecosystem processes are coupled with changes in vegetation community structure including shifts in species abundances and diversity. Characteristics of individual populations (e.g. population size, growth rates, etc.) also shift, further affecting ecosystem functioning.

The role of intraspecific variation (ITV) in ecosystem functioning is important to consider because ITV can affect extinction risk, equilibrium densities, and other factors that determine population sizes of species (Bolnick et al., 2011; Kraft et al., 2015). The amount of variation among species (i.e., interspecific variation) is often assumed to be greater than the amount within species (McGill et al.,

2006), making the effect of ITV negligible. For studies at regional and local scales that focus on individual species, however, it is important to quantify and consider ITV (Albert et al., 2011; Violle et al., 2012). The amount of ITV varies among populations (Violle et al., 2012) and can influence ecological interactions through several mechanisms including altering the number and strength of interactions among species (Bolnick et al., 2011). ITV is also an important component of community assembly (Jung et al., 2010; Laughlin et al., 2012; Siefert, 2012; Funk et al., 2017). In general, populations with high ITV have a broad niche breadth (i.e., habitat generalists) and therefore have a large geographical range, whereas populations with low ITV have a narrower niche breadth (i.e., habitat specialists) and therefore have smaller geographical ranges (Parkhurst & Loucks, 1972; Laughlin et al., 2012; He et al., 2018a). Populations with high ITV are predicted to be more resistant to environmental changes and able to keep pace with the current rate of climate change (Malyshev et al., 2016; Henn et al., 2018). Conversely, populations with low ITV may be more at risk of local extinction, leading to shifts in community composition and community-level functional traits over time. Levels of ITV may, therefore, be important for determining climate change resilience, particularly in arctic populations.

High levels of gene flow in the Arctic (Eidesen et al., 2013) may facilitate increases in ITV, potentially helping populations at risk of local extinction survive. Migration and emigration of more plastic individuals will further influence the amount of ITV that exists within a population. The role ITV plays in shifting community compositions also depends partially on the source of ITV. Whether the amount ITV within a population is fixed or plastic will determine the rate at which that population can respond to changing environmental conditions as well as how it will interact with other populations.

A functional trait-based approach to community ecology focusing on ITV is thus critical in understanding impacts from global climate change. Specifically, looking at variation in functional traits along environmental gradients will indicate how communities are affected by the environment, enabling us to make predictions on future community change (Kamiyama et al., 2014; McGill et al., 2006; Myers-Smith et al., 2019). Having a better grasp on inter-population trends in plant functional traits will provide a more complete picture of how the Arctic will respond to changing environmental conditions. Here, we investigate variation in seven functional traits for 12 arctic species across three regions spanning a latitudinal gradient (northernmost Utqiaġvik, Atqasuk, and southernmost Toolik Lake, Alaska). We aim to: (a) determine if species-level patterns across a latitudinal gradient match those of other members within the same growth form; (b) compare the distributions of trait values across regions; and (c) quantify the amount of ITV within each trait relative to the amount of variation within the growth form and across different taxonomic levels (family and species). We expect that traits will shift in response to latitude as outlined in previous literature (Table 1) for individual species as well as their corresponding growth forms. We also expect that northernmost Utqiaġvik will exhibit narrower ranges of trait values compared to more southern Atqasuk and Toolik Lake because we expect the harsher conditions at Utqiaġvik to cause individuals to converge on a single optimal trait value that promotes the greatest fitness. Additionally, we expect that the presence of more community types at Toolik Lake (i.e., more microhabitats) will have caused greater niche partitioning and therefore a wider distribution

TABLE 1 General trends in plant functional traits related to temperature as summarized in the literature

Trait		General trend
Plant height	↑	Increase with temperature in response to latitude[12], elevation[3,4,5,12], and warming[1,2,8,12]
Leaf area	↑	Increase with temperature in response to latitude[12], elevation[3,7,9], and warming[2,8,12]
Specific Leaf Area (SLA)	↑	Increase with temperature in response to latitude[12], elevation[7,9], and warming[2,8,12] but strong species-specific responses[9]
Water Band Index (WBI)	↓	Decrease with temperature in response to soil temperature[13]
Normalized Difference Vegetation Index (NDVI)	↑↓	Mixed responses to temperature in response to elevation[10] and soil temperature[11,13]
Leaf thickness	↓	Decrease with temperature in response to latitude[6,14]
Leaf Dry Matter Content (LDMC)	↓	Decrease with temperature in response to latitude[12], elevation[7,9], and warming[2,8,12]

Note: Sources include studies spanning latitudinal and elevation gradients and warming experiments. Superscripts correspond to citations supporting each trend and are listed below the table. Note: This table does not consist of a full reference list, but rather highlights the most relevant papers to our study.

[1]Baruah et al. (2017), [2]Bjorkman et al. (2018a), [3]de Villemereuil et al. (2018), [4]Gao et al. (2018), [5]Halbritter et al. (2018), [6]He et al. (2018b), [7]Henn et al. (2018), [8]Hudson et al. (2011), [9]Kichenin et al. (2013), [10]Li et al. (2016), [11]McPartland et al. (2019), [12]Myers-Smith et al. (2019), [13]Rastogi et al. (2019), [14]Wang et al. (2016).

of trait values. Finally, we hypothesize that the amount of ITV will be less than the amount of interspecific variation for all traits.

2 | METHODS

2.1 | Study area

This study included three regions spanning a latitudinal gradient stretching from the northern foothills of the Brooks mountain range to the coast of the Chukchi Sea in Alaska, USA (Figure 1). Utqiaġvik, Alaska (71°19' N, 156°36' W), the northernmost region, has been classified as high arctic tundra because of the lack of erect shrubs and abundance of sedge species. Wet meadow and dry heath communities dominate the landscape with graminoids *Carex aquatilis*, *Eriophorum* spp., and *Dupontia fisheri*, and deciduous shrubs *Salix* spp. the most common species. Utqiaġvik has a mean July temperature of ~4°C, the average precipitation during the month of July is 6.9 cm, and snowmelt occurs early to mid-June. Soils in the surrounding area were described by Bockheim et al. (2001) and generally consist of pergelic cryaquept underlain with silt and sand. Atqasuk (70°27' N, 157°24' W) and southernmost Toolik Lake (68°37' N, 149°35' W), Alaska are classified as low arctic tundra and are dominated by shrubs and sedge species. At Atqasuk dry heath, wet meadow, moist acidic (tussock tundra), and dense shrub communities are spread throughout the landscape. The most common plant species are graminoids *Carex aquatilis* and *Eriophorum vaginatum*, evergreen shrub *Vaccinium vitis-idaea*, and deciduous shrubs *Salix* spp. and *Betula*. Atqasuk has a mean July temperature of ~9°C, the average precipitation during the month of July is 7.4 cm, and snowmelt occurs in late May. Soils in the surrounding area generally consist of a combination of histic pergelic cryaquept and pergelic cryopsamment underlain with aeolian sand and silt (Komárková & Webber, 1980). At Toolik Lake dry heath, moist acidic, and dense shrub communities populate the landscape. The most common plant species are graminoids *Eriophorum vaginatum* and *Carex bigelowii*, evergreen shrubs *Ledum palustre* and *Vaccinium vitis-idaea*, and deciduous shrubs *Betula nana* and *Salix pulchra*. Toolik Lake has a mean July temperature of ~11°C, the average precipitation during the month of July is 8.8 cm, and snowmelt occurs in early to mid-May. Like Utqiaġvik and Atqasuk, the soils in the surrounding area generally consist of hydric soils within various pergelic subgroups underlain with silt (Walker et al., 1989).

The diversity of landscapes and microhabitats is largest at Toolik Lake (Walker et al., 1994), intermediate at Atqasuk (Komárková & Webber, 1980), and least at Utqiaġvik (Webber, 1978; Bockheim et al., 2001). Sampling occurred within previously established grids (Hinkel & Nelson, 2003) and near other established research plots (Wahren et al., 2005; Healey et al., 2014; Hollister et al., 2015). Soil moisture within all three regions is highly variable depending on the community type and microhabitat. The diversity of landscapes of the sampling areas matches the relative diversity of each region.

2.2 | Plant trait collection

Species were chosen for functional trait analysis based on their relative abundance at a region with special emphasis on species that occurred at all three regions. All species names are in accordance with accepted nomenclature within The Plant List (https://www.theplantlist.org/). Species that occurred across all regions include graminoids *Carex aquatilis*, *Eriophorum angustifolium*, *Eriophorum russeolum*, *Eriophorum vaginatum*, and *Luzula confusa*, forbs *Pedicularis lanata* and *Petasites frigidus*, evergreen shrubs *Cassiope tetragona* and *Vaccinium vitis-idaea*, and

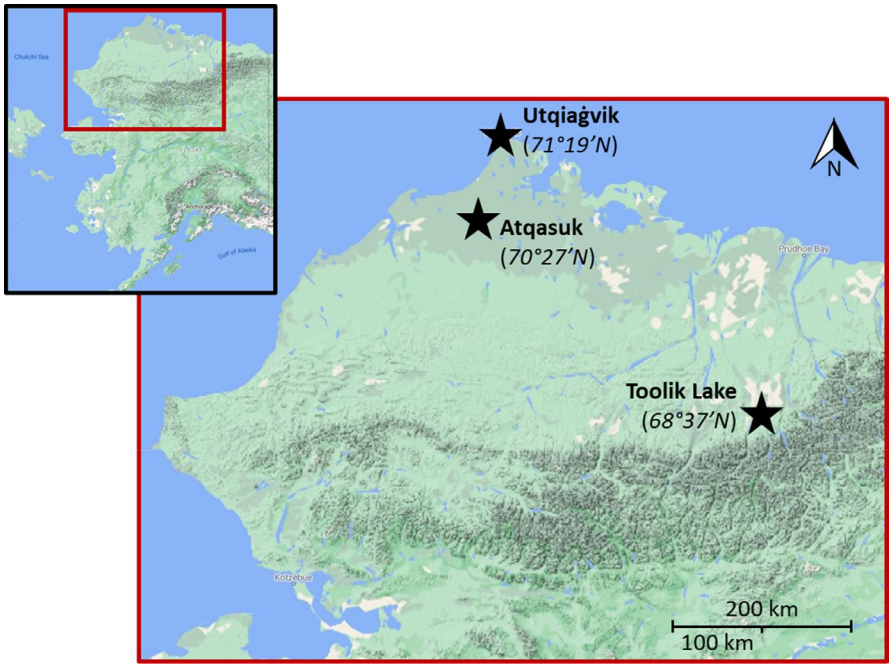

FIGURE 1 Location of study regions near Utqiaġvik, Atqasuk, and Toolik Lake, Alaska

TABLE 2 Categorical abundance of the plant species measured at each region

Species	Family	Utqiaġvik (northernmost)	Atqasuk	Toolik Lake (southernmost)
Graminoids				
Carex aquatilis	Cyperaceae	Common	Common	Common
Eriophorum angustifolium	Cyperaceae	Common	Common	Common
Eriophorum russeolum	Cyperaceae	Locally abundant	Locally abundant	Rare
Eriophorum vaginatum	Cyperaceae	Rare	Common	Common
Luzula confusa	Juncaceae	Locally abundant	Locally abundant	Locally abundant
Forbs				
Pedicularis lanata	Orobanchaceae	Rare	Rare	Rare
Petasites frigidus	Asteraceae	Common	Common	Common
Evergreen shrubs				
Cassiope tetragona	Ericaceae	Locally abundant	Locally abundant	Common
Ledum palustre	Ericaceae	*Not present*	Common	Common
Vaccinium vitis-idaea	Ericaceae	Locally abundant	Common	Common
Deciduous shrubs				
Betula nana	Betulaceae	*Not present*	Common	Common
Salix pulchra	Salicaceae	Locally abundant	Common	Common

Note: Species were classified as not present, rare, locally abundant, or common. Locally abundant species are found only in specific habitat types while common species are found in most habitats.

TABLE 3 Plant traits measured with corresponding units and replicates as well as a simplified description of how each trait was sampled

Trait	Units	Reps	Description
Plant height	cm	10	Individual was measured from the ground to the highest vegetative structure
Leaf area	cm^2	10	Calculated using ImageJ software using photographs taken on 1-cm^2 grid paper
Specific leaf area (SLA)	cm^2/g	10	Calculated by dividing the leaf area (cm^2) by its dry mass (g)
Water band index (WBI)	–	10	Collected using a single channel Unispec and calculated using Multispec software (WBI = ρ900/ρ970; ρ = reflectance)
Normalized difference vegetation index (NDVI)	–	10	Collected using a single channel Unispec and calculated using Multispec software [NDVI = (NIR − Red)/(NIR + Red)]
Leaf thickness	mm	10	Collected using a dial caliper
Leaf dry matter content (LDMC)	g/g	10	Calculated by dividing the dry mass (g) by the fresh mass (g)

Note: Replicates indicate the number of measurements taken for each species at each region.

deciduous shrub *Salix pulchra* (Table 2). Evergreen shrub *Ledum palustre* and deciduous shrub *Betula nana* were not present at Utqiaġvik but were dominant species at Atqasuk and Toolik Lake; including these two species created a more representative sample for the two southern regions. Functional traits were measured on 10 representative individuals for each species at each region. The total sampling area at each region covered about 0.1 km^2. Individuals were collected randomly across the diversity of microhabitats in which the species occurred and were spaced at least 1 m apart to prevent duplicate sampling of the same individual.

The following plant traits were measured directly on the same ten individual plants as outlined in the handbook for trait collection (Perez-Harguindeguy et al., 2016; Table 3). Plant height (cm) was the vertical distance between the ground and highest vegetative structure on the plant. Leaf thickness (mm) was measured using a dial caliper on a single, fully developed, healthy leaf with no evidence of herbivory or disease on each individual. Each leaf was photographed immediately upon returning from the field on 1-cm^2 grid paper for scale. Leaf size by area was calculated for the same leaf in which thickness was measured for each individual using ImageJ software (Schneider et al., 2012). NDVI and water band index (WBI) were calculated from reflectance measurements obtained using a single channel Unispec spectroradiometer (PP Systems, Amesbury, MA, USA). Fresh weights for each leaf were taken to the nearest milligram immediately upon returning from the field. Leaves were dried at 45°C for 48 h in a drying oven and again measured to the nearest milligram. The traits explained above were also used to calculate other traits such as SLA and LDMC.

TABLE 4 Statistical significance of differences in functional traits across regions (Utqiaġvik, Atqasuk, and Toolik Lake)

	Plant height			Leaf area			SLA			WBI			NDVI			Leaf thick			LDMC	
	df	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*
Deciduous shrubs	47	0.31	1.39	47	**<0.01**	23.0	47	0.11	2.59	46	**<0.01**	43.7	46	**<0.01**	20.1	46	**<0.01**	22.7	47	**0.01**	6.13
Betula nana	18	0.27	1.55	18	<0.01	15.5	18	**0.01**	9.47	18	**<0.01**	182	18	**<0.01**	64.4	18	**0.05**	5.38	18	0.74	0.18
Salix pulchra	27	0.32	1.33	27	**<0.01**	10.6	27	**0.02**	4.85	26	**<0.01**	88.2	26	**<0.01**	40.1	26	**<0.01**	34.0	27	**<0.01**	9.55
Evergreen shrubs	75	**<0.01**	12.5	76	0.10	2.69	76	0.82	0.24	75	0.10	2.75	77	0.40	1.07	77	**0.02**	4.81	76	**<0.01**	12.0
Cassiope tetragona	26	**<0.01**	20.3	26	0.14	2.38	27	**<0.01**	9.39	27	**<0.01**	16.6	27	0.80	0.27	27	**<0.01**	54.2	27	**<0.01**	12.9
Ledum palustre	17	**<0.01**	26.8	18	0.65	0.31	17	0.99	0.00	18	**0.01**	10.3	18	0.10	3.65	18	**<0.01**	33.4	18	**<0.01**	27.3
Vaccinium vitis-idaea	27	**<0.01**	15.4	27	**0.04**	4.05	27	**0.02**	4.76	25	**<0.01**	14.5	27	0.07	3.30	27	0.16	2.23	26	**<0.01**	11.1
Forbs	57	**<0.01**	58.3	57	**0.01**	6.14	57	**<0.01**	6.69	57	0.75	0.37	57	0.80	0.26	56	0.10	2.76	57	0.79	0.30
Pedicularis lanata	27	**<0.01**	32.3	27	**<0.01**	15.4	27	**<0.01**	32.0	27	0.31	1.40	27	0.98	0.04	27	0.20	1.92	27	0.66	0.53
Petasites frigidus	27	**<0.01**	102	27	<0.01	16.2	27	0.50	0.84	27	0.59	0.66	27	0.14	2.44	26	**<0.01**	8.59	27	**<0.01**	11.6
Graminoids	146	**<0.01**	17.3	145	**<0.01**	9.02	146	**<0.01**	13.3	144	**<0.01**	79.6	146	**<0.01**	19.6	145	**<0.01**	17.2	146	**<0.01**	15.3
Carex aquatilis	27	**<0.01**	7.87	27	0.85	0.19	27	0.21	1.84	26	0.79	0.26	27	0.10	2.92	27	**0.01**	7.25	27	0.08	3.18
Eriophorum angustifolium	26	**<0.01**	74.9	26	**<0.01**	38.1	27	**<0.01**	247	27	**<0.01**	8.72	26	**<0.01**	31.6	27	**<0.01**	15.4	27	**0.01**	5.79
Eriophorum russeolum	27	**<0.01**	35.6	26	**<0.01**	11.2	26	**<0.01**	12.3	25	**<0.01**	36.4	27	**0.01**	5.79	26	**<0.01**	36.0	27	**<0.01**	9.00
Eriophorum vaginatum	27	**<0.01**	34.4	27	**<0.01**	7.88	27	**<0.01**	17.7	27	**<0.01**	134	27	**<0.01**	8.44	26	**<0.01**	29.8	26	0.18	2.06
Luzula confusa	27	0.06	3.66	27	**<0.01**	11.2	27	**<0.01**	15.4	27	**<0.01**	65.0	27	**<0.01**	35.6	27	**<0.01**	22.7	27	**<0.01**	7.93
All species	334	<0.01	16.9	334	<0.01	8.28	335	0.15	2.11	331	<0.01	52.8	335	<0.01	16.5	333	<0.01	8.87	335	0.01	5.73

Note: Traits include plant height (cm), leaf area (cm^2), specific leaf area (SLA; cm^2/g), water band index (WBI), normalized difference vegetation index (NDVI), leaf thickness (mm), and leaf dry matter content (LDMC; g/g). Degrees of freedom (*df*), *p*-values and *F* statistics are from one-way ANOVAs; significant *p*-values (<0.05) are indicated in bold and non-significant *p*-values are in gray. Analyses were conducted for each functional group, species, and all species combined for each trait.

2.3 | Statistical analyses

All statistical analyses were performed using the R statistical software version 3.6.2 (R Core Team, 2018). Trait values more than 3.0 standard deviations away from the species trait mean at each region were identified as outliers and removed. Trait means were calculated separately for each individual species and region in order to take into account population differences. Out of 2,380 total datapoints, 21 were removed for analysis (<1% of the data). All variables were tested for normality using the Shapiro–Wilk test. Plant height, leaf area, leaf thickness, and LDMC were log-transformed to fulfill normality requirements. To identify which traits were different across regions, one-way ANOVAs were performed for each species and growth form. One-way ANOVAs for growth forms were performed with species aggregated into the appropriate growth form categories. *p*-values were adjusted for multiple comparisons using the Benjamini–Hochberg procedure.

Variance partitioning of functional traits allowed us to quantify ITV and identify at which taxonomic level the majority of variation occurred. Variance partitioning was assessed through a nested ANOVA using the varcomp function within package *ape*(Paradis & Schliep, 2019) in R. The varcompfunction first calculates the mean of each group, then compares the variance around the group mean to the mean of the next level (Messier et al., 2010; Henn et al., 2018). Variance was partitioned into growth form, family, across species, within species (across regions), and within populations (within a region).

3 | RESULTS

Plant traits varied among species and regions (Appendix S1). Populations at different regions exhibited varying ranges of trait values. For example, there was very little overlap in plant height of *Eriophorum russeolum* across the three regions. The same was true for *Petasites frigidus* and all sampled evergreen shrubs. Results from one-way ANOVA were mixed, and showed that different traits were significantly different across regions depending on the species and growth form (Table 4). All traits differed across regions for graminoids ($p < 0.01$) and five traits differed across regions for deciduous shrubs ($p < 0.01$). All traits differed across regions for at least six species ($p < 0.05$). For all species combined, all traits except SLA differed across regions.

Trends in individual species across regions often varied within a growth form. For example, the overall net change in SLA for deciduous shrubs was insignificant ($p = 0.11$). However, within the growth form deciduous shrubs SLA significantly increased from north to south for *Salix pulchra* ($p = 0.02$), but significantly decreased for *Betula nana* ($p = 0.01$) (Table 4; Figure 2). In other cases, a single species drove the overall growth form response. For example, LDMC decreased from north to south for *Salix pulchra* ($p < 0.01$) which mirrors the response for deciduous shrubs ($p = 0.01$), but the response for *Betula nana* ($p = 0.74$) was insignificant.

Kernel density plots showed a large amount of overlap in the distribution of functional traits across regions (Figure 3), in contrast with the trends in functional traits for each individual species which often showed significant differences between regions (Table 4; Appendix S1). In general, however, northernmost Utqiaġvik had a narrower distribution of traits than more southern Atqasuk and Toolik Lake. Differences in trait distributions within WBI were especially apparent, with a much larger distribution within more southern Atqasuk and Toolik Lake and a much narrower distribution within northernmost Utqiaġvik. Similar trends are found within NDVI and LDMC.

Results from the nested ANOVA varied greatly among traits. Differences within a species across regions accounted for most of the variation within WBI (68.6%; Figure 4) while variation at the population level accounted for most of the variation within NDVI (54.7%). Conversely, population within a region accounted for little of the total variation within plant height (10.3%), leaf area (9.0%), SLA (15.4%), and leaf thickness (14.4%). The total amount of ITV for a species (the "population" and "within species" levels combined) was smaller than the amount of interspecific variation (the "across species," "family," and "growth form" levels combined) in all traits except WBI and NDVI. Family accounted for relatively small portions of total variation for most traits (0–15% for all traits except leaf area, which was 32.4%), but growth form accounted for much of the variation within plant height (38.7%), SLA (64.0%), and LDMC (39.3%).

4 | DISCUSSION

4.1 | Species trends in traits across a latitudinal gradient

General trends in functional traits across the latitudinal gradient were consistent with previous findings. Plant height and leaf area were larger in the southern populations for most species. Increased plant size with temperature is common in most studies and is attributed to slower growth rates restricted by colder temperatures (Caldwell et al., 1978; Bjorkman et al., 2018a; Gao et al., 2018; Hudson et al., 2011; de Villemereuil et al., 2018). Responses to NDVI were extremely species-specific, which aligns with studies showing both browning and greening trends throughout the Arctic (Li et al., 2016; McPartland et al., 2019; Rastogi et al., 2019). Species also showed differing responses in SLA and LDMC, two traits that are opposite in the leaf economics spectrum (Díaz et al., 2016). Some species, such as *Salix pulchra*, showed an increase in SLA with a respective decrease in LDMC from north to south along the latitudinal gradient. Other species, such as *Betula nana*, showed a decrease in SLA with a respective increase in LDMC from north to south along the latitudinal gradient. Previous studies have shown that changes in SLA and LDMC are more apparent at wetter than drier regions (Baruah et al., 2017; Bjorkman et al., 2018a). Large differences in soil moisture across regions may, therefore, explain why trends were inconsistent for some traits and species. Results for WBI, for example, suggest that the middle region (Atqasuk) may have been

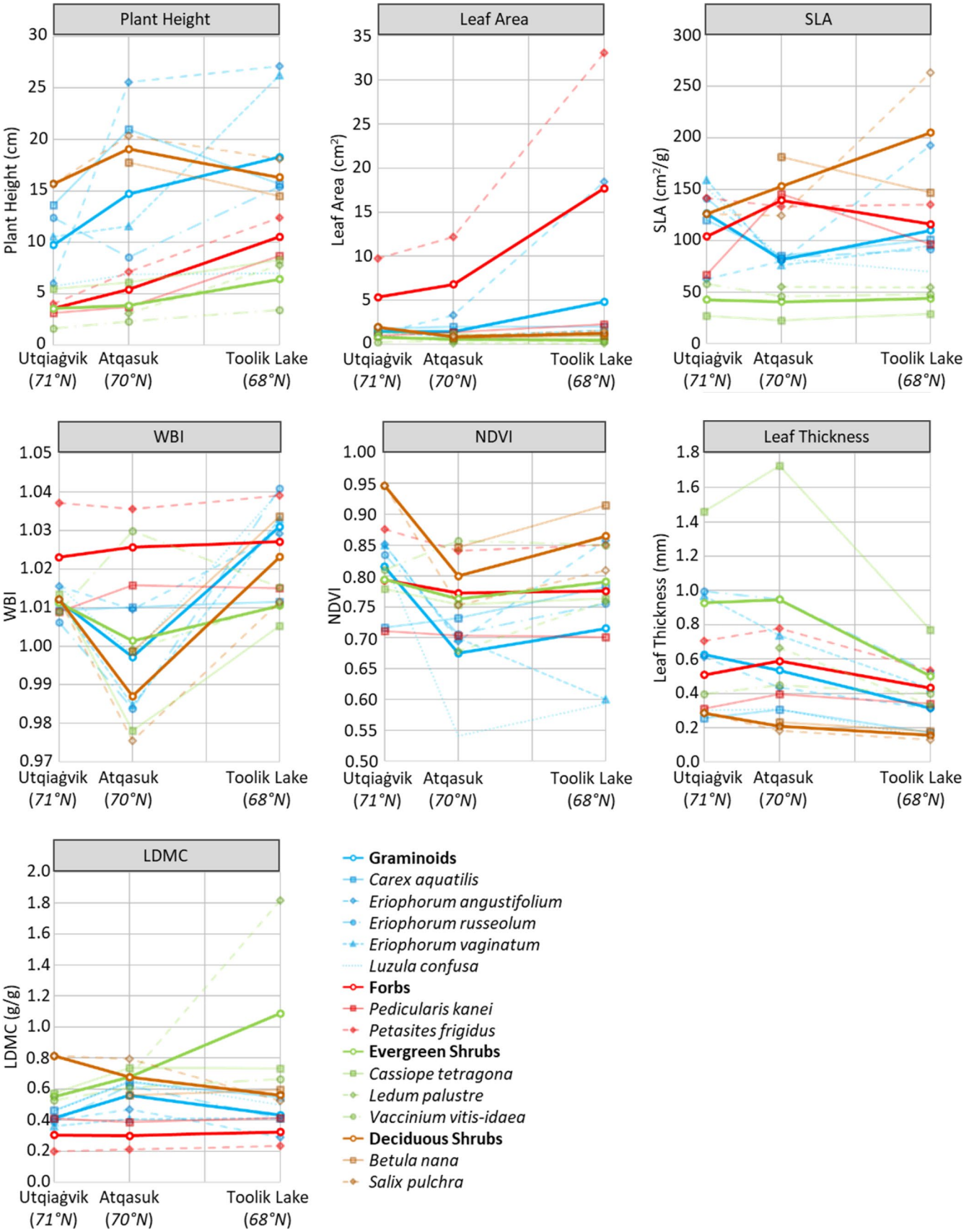

FIGURE 2 Comparison of species-level average trait values with growth forms for seven functional traits and three populations at the three regions spanning a latitudinal gradient (northernmost Utqiaġvik, Atqasuk, and southernmost Toolik Lake). Dashed lines represent individual species and solid lines represent growth forms. Colors correspond with growth forms

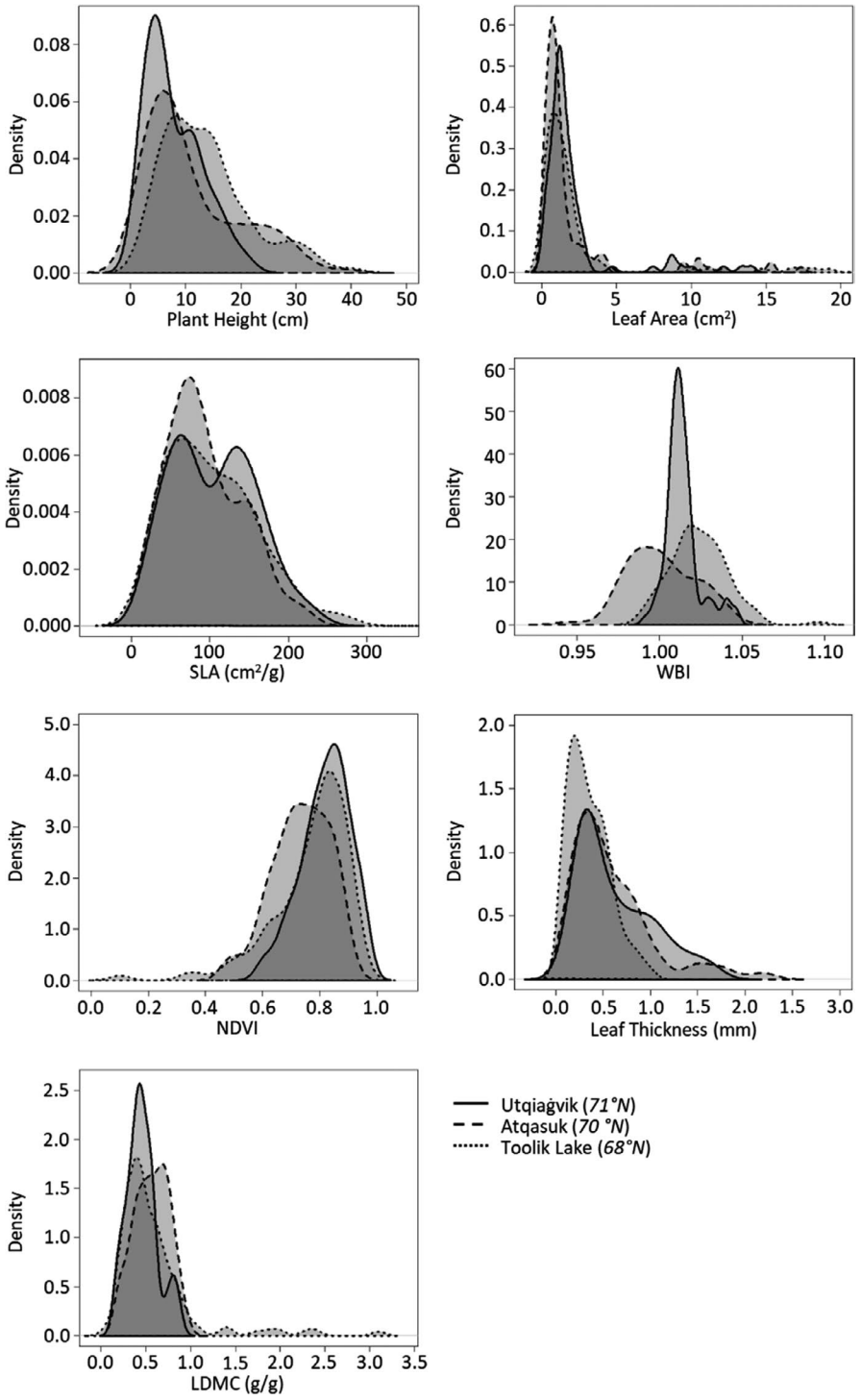

FIGURE 3 Kernel density plots for seven functional traits across three regions: northernmost Utqiaġvik (solid line), Atqasuk (dashed line), and southernmost Toolik Lake (dotted line). Kernel density plots allow visualization of data without assuming normality, thus providing distributions by smoothing out the noise

substantially drier where sampling took place. Many species showed a significant drop in WBI between Utqiaġvik and Atqasuk, but a significant increase in WBI between Atqasuk and Toolik Lake. Since this study takes place at the regional scale rather than the local scale, effects of community type (largely a response to soil moisture) on results are masked. Individuals collected from multiple community types (e.g. *Carex aquatilis*) were grouped together for analysis. Future studies incorporating differences in variation and trait means across community types would better reflect what role ITV plays in temperature-trait relationships.

Contrasting results in species responses within a growth form to environmental changes along a latitudinal gradient shown here supports results of previous work, which also suggest that the traditional approach of grouping species by growth form may be insufficient in describing community-level changes (Kamiyama et al., 2014; Saccone et al., 2017; Thomas et al., 2019). Saccone et al. (2017) showed especially strong species-specific responses in deciduous shrubs, which mirrors our own findings (our results showed *Salix pulchra* and *Betula nana* having opposite trends SLA and LDMC). Using a latitudinal gradient as a space-for-time substitution to investigate

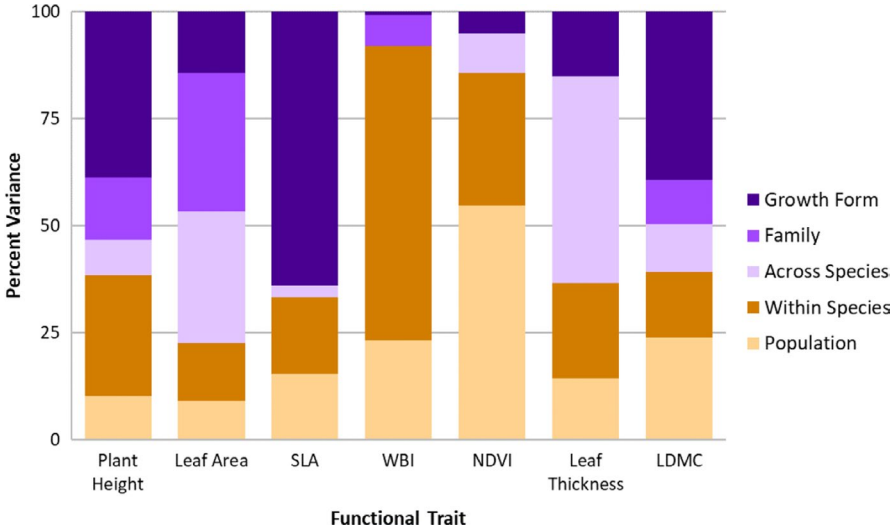

FIGURE 4 Variance partitioning within populations (within a region) and within species (across regions; shades of orange), and across different taxonomic levels (shades of purple) for seven plant functional traits: plant height (cm), leaf area (cm^2), specific leaf area (SLA; cm^2/g), water band index (WBI), normalized difference vegetation index (NDVI), leaf thickness (mm), and leaf dry matter content (LDMC; g/g). Percent variance results are from a nested ANOVA comparing variance around one group mean to the mean of the next level. Intraspecific variation (ITV) can be interpreted by summing the "within species" and "population" sections. Interspecific variation can be interpreted by summing the "across species," "family," and "growth form" sections. Results are constrained by the uneven amount of sampling across groups (for example a limited number of species of the same family); however, they are revealing and show major differences in variance partitioning among traits

species-specific responses to changing environmental conditions will help better our understanding of how overall ecosystem functioning will change.

Species abundance should also be considered when observing trends in functional traits. Species with higher relative abundances have a stronger effect on ecosystem functioning (Baruah et al., 2017). The sedge *Carex aquatilis* is the most abundant species at Utqiaġvik; however, if Utqiaġvik's plant community shifts to resemble the more southernly regions of Atqasuk and Toolik Lake, *Eriophorum vaginatum* and deciduous shrubs will dominate the landscape. Compared to *Carex aquatilis*, deciduous shrubs *Betula nana* and *Salix pulchra* have considerably higher SLA and NDVI. SLA has been shown to positively correlate with relative growth rates (Reich et al., 1992) and NDVI has been shown to positively correlate with primary productivity (Sellers, 1985); greater abundances of species that possess these trait values may, therefore, affect rates of carbon exchange in arctic communities.

Shifts in plant traits for common species may, therefore, be more indicative of how the ecosystem will respond to changing environmental conditions. Soudzilovskaia et al. (2013) showed evidence that plant traits predict relationships between species abundance and temperature, suggesting selection for specific traits rather than species under certain environmental conditions. Other studies have also shown that functional traits are strong predictors for community assembly (Alsos et al., 2007; Laughlin et al., 2012; Henn et al., 2018). The specific values of traits are determined by environmental conditions and the relationships between related traits. Díaz et al. (2016) described how various traits are related to each other by demonstrating that three-quarters of trait variation is captured along two axes that describe plant form and function: one that describes overall plant size and one that describes the leaf economics spectrum. The relationship between these two spectrums indicate that combinations of traits exhibit trade-offs and contribute to the overall fitness of the plant. For example, in this study deciduous shrubs *Betula nana* and *Salix pulchra* showed opposite trends in SLA and LDMC along the latitudinal gradient, which are opposite traits in the leaf economics spectrum (Díaz et al., 2016). Trade-offs in traits are crucial in determining how plants adapt to their environment. The relationships among functional traits, environmental conditions, and species abundances all play a role in ecosystem interactions, and understanding these relationships is critical in predicting future ecosystem change.

4.2 | Intraspecific variation in functional traits

The amount of variation between species has often been assumed to be greater than the amount of variation within species (Albert et al., 2011; Bolnick et al., 2011; Henn et al., 2018), but previous research has shown that different populations of species can have different mean trait values (Violle et al., 2012; Funk et al., 2017); this is reflected in our samples (Appendix S1) resulting in larger amounts of ITV than interspecific variation for some traits (Figure 4). While the results of variance partitioning are constrained by the set of species included (and their representation of growth forms and families is uneven) the comparisons across traits are equally constrained and show large differences (Figure 4). Of the families included in our sampling, only two include more than a single species (Table 2). The

sedge family (Cyperaceae) is the most abundant plant family in the tundra (Small & Cayouette, 2016) and includes four of our sampled species, so observing how much of the observed variation in our samples is attributed to this family as well as other common families (i.e., Ericaceae) indicates whether species that are closely related have similar trait values.

Our sampling methods were designed to capture the total amount of variation that exists within each region for the selected species; which, based on the species sampled, also provides information within and across plant growth forms. By sampling individuals randomly across the landscape instead of focusing on specific community types, we were able to collect individuals of the same species growing in different conditions (e.g. differences in soil moisture, vegetation community type, etc.) in order to capture the greatest amount of variation that exists at each region. Quantifying ITV levels and comparing it across species and regions is important to help explain the impact the species has on the community as a whole such as interspecies interactions (i.e., competition) and plant performance (McGill et al., 2006).

Differences within a population (within a region) accounted for more than 50% of the total variation in one functional trait (NDVI). High amounts of ITV in NDVI can be at least partially attributed to differences in age (particularly for deciduous and evergreen shrubs). Leaf age has been shown to correlate with chlorophyll content, which is closely related with NDVI (Koike, 1990; Jones et al., 2007). Including both new and old leaves in each region's sample would add to the total amount of variation for that species. Variation in NDVI could also be attributed to differences in nutrients at the different regions and microhabitats (Cabrera-Bosquet et al., 2011). Variance partitioning across taxonomic levels also differed greatly for each functional trait. Within species differences across regions accounted for most of the variation within WBI. WBI has been shown to correlate with leaf water content (Peñuelas et al., 1993) which could be indicative of differing environmental conditions (i.e., soil moisture). For SLA and LDMC, growth form accounted for most of the variation. Both SLA and LDMC have been established as important indicators of leaf strategies; leaves with low SLA and high LDMC have better resource retention, which is important in resource-poor environments such as the Arctic (Reich et al., 1992; Wilson et al., 1999). Little ITV within SLA and LDMC suggests that a single set of trait values is optimal for each species, but that these values are different for each growth form. More variation across growth forms for SLA and LDMC suggests that resource acquisition strategies change more with growth strategies than with individual species.

The role ITV plays in community ecology is complex and often ignored in functional trait-based studies (Siefert et al., 2015; Funk et al., 2017). ITV is associated with niche breadth (Sides et al., 2014), and one hypothesis is that harsh environments cause populations to converge on a single optimal trait value that best reflects plant performance under those environmental conditions as long as there is no migration from other populations with significantly different conditions (i.e., the trait convergence hypothesis; Fukami et al., 2005; Laughlin et al., 2012; Henn et al., 2018). The trait convergence hypothesis also predicts divergence from a mean trait value in instances where high levels of community organization have arisen (Fukami et al., 2005; de Bello et al., 2009; Pillar et al., 2009; Henn et al., 2018). The process of community assembly is very complex with elements that are stochastic in nature, but the trait convergence hypothesis can help inform predictions of how different communities behave and potentially evolve over time. Based on these predictions, we hypothesized that harsher conditions at northernmost Utqiaġvik would cause individuals to follow the pattern of trait convergence and that more optimal conditions at southernmost Toolik Lake would facilitate trait divergence and thus niche partitioning. Additionally, the presence of fewer community types at Utqiaġvik (i.e., the landscape is more homogenous) and more community types at Toolik Lake (i.e., the landscape is more heterogenous) would lead to greater variation at Toolik because of the presence of more microhabitats. Kernel density plots showing the spread of functional traits for each region, however, do not support this hypothesis (Figure 3). WBI, NDVI, and LDMC follow the pattern outlined in our hypothesis, but most other traits show similar amounts of variation across regions. Our study regions might be too close together to see obvious differences in trait variability; a larger geographical scale might better support the trait convergence hypothesis.

4.3 | Future directions

Plant functional traits (and more specifically, combinations of traits) have already been shown to be linked with ecosystem processes such as primary productivity, litter decomposition, and carbon storage and sequestration (Reich et al., 1999; Díaz et al., 2016). If our use of a latitudinal gradient as a space-for-time substitution proves to be indicative of future environmental change caused by rising global temperatures, then we can expect the Arctic to experience general increases in plant height and leaf area and decreases in leaf thickness. Most shifts in functional traits will likely occur within graminoids and deciduous shrubs, as these two functional groups showed the greatest number of significant changes with latitude in our results. Species within these two growth forms may exhibit individualistic responses to increased temperature over time (e.g. deciduous shrubs *Betula nana* and *Salix pulchra* showed opposite trends in multiple traits across a latitudinal gradient), which supports the need for studies focusing on specific species rather than growth forms. Plant height, leaf area, and leaf thickness all have the potential to increase the net primary productivity of plant communities, which coupled with increased decomposition suggested by other studies (McLaren et al., 2017; Parker et al., 2018) has the potential to offset the rate of carbon exchange in the Arctic. Studying long-term shifts in functional traits in real time is, therefore, critical in fully understanding how ecosystem functioning in the Arctic will change.

Establishing more long-term functional trait datasets will help determine how traits are shifting with changing environmental conditions. While many trait-based studies have been conducted on a

very broad geographical scale (Reich et al., 1999; Díaz et al., 2004; Wright et al., 2005; Díaz et al., 2016), few studies have been conducted over a temporal scale (although see Tolvanen & Henry, 2001; Baruah et al., 2017; Bjorkman et al., 2018b). Establishing how functional traits shift in response to long-term environmental manipulations will help predict changes in ecosystem functioning over time.

Finally, establishing the amount of gene flow and genetic variation in arctic populations is key to determining whether they are locally adapted to their environment or are demonstrating phenotypic plasticity (Abbott et al., 1995; Gabrielsen et al., 1997; Post et al., 2013; Birkeland et al., 2017; Bjorkman et al., 2017). Some studies have suggested the amount of ITV in different populations may be linked with levels of phenotypic plasticity (Kichenin et al., 2013; He et al., 2018a; Henn et al., 2018), but there is little evidence to support this hypothesis. It is likely that populations experience a combination of local adaptation and phenotypic plasticity, and that plasticity itself is an adaptive trait. Without determining rates of local adaptation, however, it is difficult to predict just how plant communities will respond to changing environmental conditions. Implementing more wide-spread reciprocal transplant experiments will help reconcile the local adaptation versus plasticity debate, and advance our knowledge of plant–climate interactions (Schwaegerle et al., 2000; Bjorkman, 2013; Halbritter et al., 2018; de Villemereuil et al., 2018).

4.4 | Conclusions

Whether species trends in functional traits across a latitudinal gradient mirrored those of their corresponding growth forms depended on the trait. Some traits, such as plant height, leaf area, and leaf thickness, showed fairly consistent trends across all species and growth forms between the northernmost and southernmost regions. Plants generally had increased height and leaf area and decreased leaf thickness in the southern populations compared to the northern populations. Other traits showed highly variable patterns, such as SLA, which showed opposite patterns between species within the same growth form category. These results highlight the need for species-focused rather than growth form-focused studies.

Additionally, there was large overlap in distributions of most functional traits across the three regions. For some traits, however, regions showed distinctively different trait distributions. Northernmost Utqiaġvik had much narrower trait distributions for WBI, NDVI, and LDMC than the two southern regions (Atqasuk and Toolik Lake). Traits also varied in how much ITV they displayed. Most of the variation within WBI and NDVI was found within the population (within the region) or within the species across regions (i.e., intraspecific variation). For all other traits, however, the variation within a species (ITV) was much less than the variation between species. Our results further emphasize the fact that the amount of ITV in traits can be highly variable, and therefore should be measured and accounted for in trait-based studies at the local and regional scales.

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AUTHOR CONTRIBUTIONS

KB designed the study and led data collection with JM; KB wrote manuscript with RH; KB conducted statistical analysis; RH, JM, and SO advised in revisions for the manuscript; RH and SO secured funding for the project and SO offered logistical support.

DATA AVAILABILITY STATEMENT

Functional trait data was submitted to the Tundra Trait Team (TTT) and will be included in version 2 of the database. Functional trait data are also publicly available on Figshare (https://doi.org/10.6084/m9.figshare.14511987.v1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Box and whisker plots for seven plant functional traits and twelve species across three regions in northern Alaska.

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