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RESEARCH ARTICLE

Geomorphological processes shape plant community traits in the Arctic

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Abstract

Aim: Geomorphological processes profoundly affect plant establishment and distributions, but their influence on functional traits is insufficiently understood. Here, we unveil trait–geomorphology relationships in Arctic plant communities.

Location: High-Arctic Svalbard, low-Arctic Greenland and sub-Arctic Fennoscandia.

Time period: 2011–2018.

Major taxa studied: Vascular plants.

Methods: We collected field-quantified data on vegetation, geomorphological processes, microclimate and soil properties from 5,280 plots and 200 species across the three Arctic regions. We combined these data with database trait records to relate local plant community trait composition to dominant geomorphological processes of the Arctic, namely cryoturbation, deflation, fluvial processes and solifluction. We investigated the relationship between plant functional traits and geomorphological processes using hierarchical generalized additive modelling.

Results: Our results demonstrate that community-level traits are related to geomorphological processes, with cryoturbation most strongly influencing both structural and leaf economic traits. These results were consistent across regions, suggesting a coherent biome-level trait response to geomorphological processes.

Main conclusions: The results indicate that geomorphological processes shape plant community traits in the Arctic. We provide empirical evidence for the existence of generalizable relationships between plant functional traits and geomorphological processes. The results indicate that the relationships are consistent across these three distinct tundra regions and that geomorphological processes should be considered in future investigations of functional traits.

KEYWORDS
cryoturbation, deflation, fluvial processes, microclimate, plant functional traits, solifluction, tundra, vegetation

1 | INTRODUCTION

Geomorphological processes shape ecosystems fundamentally, because they provide a diversity of habitats by eroding and relocating rocks, sediments and soils (French, 2017). From the perspective of a plant, these processes alter resource availability, cause mechanical disturbance and damage, and increase soil instability (Becher et al., 2018; Giblin et al., 1991; Virtanen et al., 2010). Geomorphological processes control, in part, the recruitment of plant species (Frost et al., 2013; Sutton et al., 2006), their occurrence and richness patterns, in addition to community composition (Giaccone et al., 2019; le Roux, Virtanen, et al., 2013). These processes also influence the outcome of biotic interactions (Gentili et al., 2013) and provide refugia (Millar et al., 2015). However, we know very little about how geomorphological processes influence plant functional traits (see our systematic literature review in Appendix S1, Table S1; Figure S1) and even less about these relationships in the Arctic tundra (see Apple et al., 2019; Kopanina et al., 2020 for alpine tundra).

Plants and their functional traits form the core of terrestrial ecosystems (Díaz et al., 2016; Wright et al., 2004). The above-ground functional traits vary chiefly on two main axes: the size–structural trait axis (e.g., plant height, leaf area) and the leaf economic trait axis (e.g., leaf nutrient contents, specific leaf area) (Díaz et al., 2016; Wright et al., 2004). The first is related, for instance, to carbon storage size (Cahoon et al., 2012; Chapin et al., 2005), and the latter to nutrient cycling and photosynthetic efficiency (Diaz et al., 2004; Reich, 2014). In tundra ecosystems, functional trait–environment relationships form consistent and generalizable patterns (i.e., plant communities from the Arctic to Antarctic have similar responses to microclimate, soil moisture and soil chemistry; Kemppinen et al., 2021), yet their responses to other environmental variables, such as geomorphological processes, have gained less attention. Overall, the functional trait compositions have changed in the tundra plant communities over the last decades, and especially, size–structural traits have been linked to the drastic biome-wide warming (Bjorkman, Myers-Smith, Elmendorf, Normand, Rüger, et al., 2018).

In the Arctic, temperatures, wind, snow and hydrological conditions are rapidly changing (IPCC, 2018), and Arctic geomorphology is responding. For instance, suitable conditions for cryogenic processes might be lost by the end of this century (Aalto et al., 2017); aeolian processes have expanded and increased in magnitude (Bullard & Mockford, 2018; Heindel et al., 2017), and fluvial processes are shifting from snowmelt driven to more rainfall driven (Beel et al., 2021; Bintanja & Andry, 2017). In light of these changes, an important yet unanswered question is: How will Arctic plant communities, especially their functional traits, respond to changes in geomorphological processes? Functional traits provide information on the global carbon cycle, to which Arctic vegetation contributes disproportionately (Cornelissen et al., 2007; Happonen et al., 2022; Pearson et al., 2013). Thus, it is important to quantify trait–geomorphology relationships in the Arctic, because both plant functional traits (Bjorkman, Myers-Smith, Elmendorf, Normand, Rüger, et al., 2018) and geomorphological systems are facing major shifts in response to changing climatic conditions.

Here, we explore the relationship between plant traits and four geomorphological processes common in Arctic ecosystems: cryoturbation, deflation, fluvial processes and solifluction (Figure 1). Overall, geomorphological process activity is controlled by climate, and it can have distinct characteristics in the Arctic (French, 2017). For example, aeolian processes, such as deflation, move fine soil material and are intensified during winter, when wind speeds are high and the ground surface is desiccated (Heindel et al., 2018). In contrast, at the start of the growing season, snowmelt increases fluvial processes, which erode and accumulate sediments (Goudie, 2006). Solifluction is slow mass wasting of the topsoil, and it is especially active in Arctic soils, owing to their high moisture content and both diurnal and seasonal freezing cycles and the presence of permafrost (Jaesche et al., 2003; Matsuoka, 2001). Cryoturbation is the mixing and relocation of soil material caused by seasonal freezing and thawing (Hjort, 2014). Consequently, all these processes influence vegetation cover (D'Amico et al., 2015) and dynamics (Becher et al., 2018; Virtanen et al., 2010). Therefore, we expect to find that trait–geomorphology relationships differ between structural and leaf economic traits, because some processes are more related to soil resources, whereas others are more related to physical disturbance

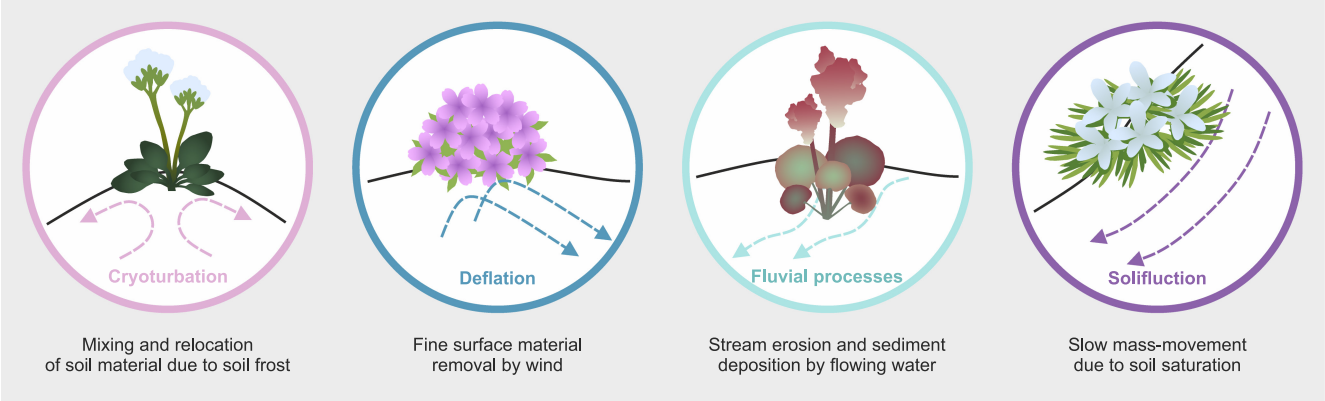

FIGURE 1 Geomorphological processes of the study

of plant growth and development. We use this information to showcase how traits might respond to changes in the magnitude of geomorphological processes.

2 | MATERIALS AND METHODS

2.1 | Study design

We surveyed 5,280 plots within 33 study grids at three sites: six grids in the high-Arctic site, six in the low-Arctic site, and 21 in the sub-Arctic site. Each grid was 8 m × 20 m and contained 160 study plots (1 m^2) (photographs of example grids are in Figure S2). We located the study grids within the sites along topographic and vegetation gradients to maximize environmental variation within each site and each grid. The grids were located outside anthropogenic activities, such as hiking trails. At each site, the grids were located close to each other; the maximum distance between grids was 3.75 km at the high-Arctic site, 1.05 km at the low-Arctic site, and 2.60 km at the sub-Arctic site. From each plot, we collected the vascular plant and environmental data. The species data consist of 61 species from the high-Arctic site, 75 from the low-Arctic, and 134 from the sub-Arctic. Altogether, the species data consist of 200 species (Table S2).

2.2 | Study sites

2.2.1 | High-Arctic site

The high-Arctic site was located on the slopes of Adventdalen and Endalen in Svalbard (Table 1). The plant species and environmental data were collected during the growing season of 2018. The dominating species at the site were *Dryas octopetala*, *Salix polaris* and *Cassiope tetragona* and, to a lesser extent, *Bistorta vivipara*, *Festuca rubra* and *Poa pratensis*. All grids at the site were under similar grazing pressure (mainly *Rangifer tarandus platyrhynchus* and Anserinae ssp.).

2.2.2 | Low-Arctic site

The low-Arctic site was located on the highland of Ammalortup Nunaa in western Greenland (Table 1). The plant species and environmental data were collected during the growing season of 2018. The dominating species at the site were *Vaccinium uliginosum*, *Betula nana* and *Salix glauca* and, to a lesser extent, *Cassiope tetragona*, *Salix herbacaea* and *Rhododendron tomentosum*. All grids at the site were under similar grazing pressure (mainly *Ovibos moschatus* and *Rangifer tarandus groenlandicus*).

2.2.3 | Sub-Arctic site

The sub-Arctic site was located on Mount Saana in north-western Fennoscandia (Table 1). The plant species data were collected during the growing seasons of 2011–2013, and the environmental data during the growing season of 2013. The dominating species at the site were *Empetrum hermaphroditum*, *Betula nana* and *Juniperus communis* and, to a lesser extent, *Vaccinium vitis-idaea*, *Vaccinium uliginosum* and *Vaccinium myrtillus*. All grids at the site were under similar grazing pressure (mainly *Rangifer tarandus tarandus* and *Cricetidae* sp.).

2.3 | Plant data

We combined field data on vascular plant species occurrences with database records of seven plant functional traits, namely plant height, specific leaf area, seed mass, leaf dry mass content, leaf area, leaf nitrogen content and leaf phosphorus content (following Kemppinen et al., 2021). Initially, we identified the species and estimated their percentage coverage in the field (see full species list in Table S2). Then, we extracted trait observations for the identified species from three databases: the Tundra Trait Team database (TTT), the TRY Plant Trait Database (TRY) and the Botanical Information and Ecological Network (BIEN) (Bjorkman, Myers-Smith, Elmendorf, Normand, Thomas, et al., 2018; Kattge et al., 2020; Maitner et al., 2018). We provide a full citation list of the trait data in the Appendix A and in the (Appendix S1).

TABLE 1 Site descriptions

Description	High-Arctic site	Low-Arctic site	Sub-Arctic site
Location	78.20 N, 15.73 E	66.95 N, −50.72 W	69.05 N, 20.81 E
Elevation (m a.s.l.)	30–110	520–560	595–810
Mean annual temperature (°C)	−5.9	−4.9	−3.1
Annual precipitation sum (mm)	196	252	518

Note: The climate data at the high-Arctic site are based on the years 1971–2000 measured at the Svalbard Airport observation site (78.25 N, 15.50 E; 28 m a.s.l.; 7.7 km from the study site) (Norwegian Centre for Climate Services, 2019), at the low-Arctic site on the years 1977–2013 measured at the Kangerlussuaq Airport (67.02 N, −50.70 W; 50 m a.s.l.; 7.0 km from the study site) (Danish Meteorological Institute, 2019), and at the sub-Arctic site on the years 1991–2018 measured at the Saana meteorological station (69.04 N, 20.85 E; 1,002 m a.s.l.; 1.5 km from the study site) (Finnish Meteorological Institute, 2019b) and the Kyläkeskus meteorological station (69.04 N, 20.80 E; 480 m a.s.l.; 1.0 km from the study site) (Finnish Meteorological Institute, 2019a).

We used the species names and their widely used synonyms to extract trait observations from TTT, TRY and BIEN. The observations we derived from TRY correspond to trait identity (ID) numbers here in parentheses: leaf area (3108, 3109, 3110, 3111, 3112, 3113 and 3114), leaf area for species with compound leaves (3108, 3110, 3112 and 3114), plant height (3106), seed mass (26), leaf dry matter content (47), leaf nitrogen content (14), leaf phosphorus content (15) and specific leaf area (3115, 3116 and 3117). In addition, we extracted observations from TRY for species that occurred in the TTT database and in Fennoscandian countries (based on occurrence records of the Global Biodiversity Information Facility; GBIF; https://www.gbif.org/). Furthermore, we searched for records from all genera within our dataset from BIEN. We standardized the nomenclature to match the GBIF backbone nomenclature.

Chiefly, we followed the methods described by Bjorkman, Myers-Smith, Elmendorf, Normand, Thomas, et al. (2018) to clean and combine the trait data. We determined the error risk of each observation by calculating by how many standard deviations (*SDs*) the value differs from the mean values of the given species and trait (the focal observation excluded in the *SD* and mean calculations). We used an error risk threshold of three, except: (1) if there were fewer than four trait observations, we included all data; and (2) if there were <10 trait observations, we included only those with an error risk <2.25. In addition, we used expert knowledge to exclude manually any trait values that we considered to be impossible for some species. For instance, we considered that a 10-m-tall individual of *Juniperus communis* is not possible in tundra ecosystems.

We used species-level trait observations; however, if a given species lacked this, we used genus-level trait observations. Initially, we selected georeferenced observations within the tundra climatic zone (class "ET" in the study by Beck et al., 2018). Then, we averaged the trait values over the species within the genus. Finally, we had trait observations at the species level, and in addition, at the genus level, if there were no species-level trait observations available.

We calculated community-weighted mean (CWM) values for the 5,280 plots. The responses of functional traits to environmental conditions are often investigated by using CWM values, in which the species-level average trait value is weighted by the species abundance (Lavorel et al., 2007). Here, we used hierarchical sampling and bootstrapping, and we accounted for the varying relevance of the trait observation for tundra vegetation and the intraspecific variation in the trait data. We used an adjusted version of the code that is available at: https://github.com/richardjtelford/traitstrap (Maitner et al., 2021). If a given trait observation was georeferenced, we used these location data to extract information on the climate in which the observation was made using a fine-scale climate classification (Beck et al., 2018). Initially, we classified the relevance of a given trait observation by using five nested hierarchies: (1–3) Köppen–Geiger climate classifications; (4) the georeferencing information; and (5) the global level, in which all trait observations were included. Consequently, a given trait observation received a five times higher weight (1–5) if it was a georeferenced trait observation recorded within the tundra climate class instead of a non-georeferenced global-level trait observation. Finally, we used these weights (1–5) to take a random sample of the trait observations in order to calculate the CWM values for the plots. We repeated this 100 times for a given plot to quantify how CWM values might be influenced by the intraspecific variation within the trait data. We included CWM values in the analyses only if the trait data (at the species or genus level) were available for the species that comprised a minimum of 90% of the vegetation cover in a given plot. On average, the species-level trait observations covered 96.0% (seed mass) to 99.5% (plant height) of the species that were weighted by their abundance in the plots. The coverage increased to 99.1% and 99.9%, respectively, when we also included the genus-level trait observations. On average, the number of trait observations per species weighted by their abundance in the plots varied from 32.9 (seed mass) to 667.0 (plant height), indicating that the common species are also common in the trait data.

Species reproducing by spores (i.e., ferns and lycopods) instead of seeds were excluded from the CWM seed mass calculations. However, only 34% of the plots had any fern and/or lycopod species present, and <1% of the plots had relative fern and/or lycopod cover >25% (of the total vegetation cover). Therefore, ferns and lycopods do not contribute greatly to the CWM trait values.

We used $\log_{10}$-transformations for CWM trait values in our analyses.

2.4 | Environmental data

In this study, we focus on geomorphological processes that represent relatively slow and persistent geomorphological activity, not rapid event-type disturbances. Therefore, although we mapped the processes only at a given point in time, the recorded processes are likely to represent decadal activity patterns affecting long-living Arctic plant life. The geomorphological processes were recorded for each plot *in situ* by a geomorphologist (following methodology of Virtanen et al., 2010). In the high-Arctic and low-Arctic sites, the survey was carried out by J.K. in 2018, and in the sub-Arctic site by M.L. in 2013. First, the geomorphologist identified whether the plot was affected by any Earth surface process. Second, the type of the process was recorded. Third, the geomorphologist estimated the proportion of the plot surface where the given process affected the topsoil (coverage 0–100%). At all three sites, four types of processes were present, namely cryoturbation, deflation, fluvial processes and solifluction. Cryoturbation was identified by landforms that had been created and shaped by soil frost (i.e., freeze–thaw processes), such as patterned ground and earth hummocks. Deflation was identified by signs of wind erosion on the soil surface (i.e., fine material had been blown out). Fluvial processes were identified by marks of stream erosion and sediment deposition. Solifluction was identified by landforms that had been formed by slow mass movement of water-saturated soils, such as solifluction terraces and lobes.

Soil moisture was measured as the volumetric water content (VWC%) using a hand-held time-domain reflectometry sensor

(Spectrum Technologies FieldScout TDR 300). We used 10 cm probes at the low-Arctic site and 7.5 cm probes in the two other sites. The measurements capture the general pattern of the relative moisture conditions across each site (following methodology by le Roux, Aalto, et al., 2013). We measured soil moisture on days without precipitation for ≥24 h prior. We measured soil moisture at three points within each plot to account for within-plot soil moisture variation, and we used the mean of these three points to represent the soil moisture conditions at the plot. We measured soil moisture once at the high-Arctic (8 August 2018), once at the low-Arctic site (9 July 2018) and three times at the sub-Arctic site (12–13 June, 23–24 July and 9 August 2013). For the sub-Arctic site, we used the mean soil moisture value of the three measurements to represent the soil moisture conditions in the analyses.

Soil pH was analysed from soil samples. Initially, we collected 72 samples at the high-Arctic sites and at the low-Arctic sites (12 samples per grid) and 378 samples at the sub-Arctic site (18 samples per grid). We then oven-dried the samples at 40°C and determined their pH from a 1:5 suspension of soil in a solution of distilled water and $CaCl_2$ (0.01 mol/L), following the International Organization for Standardization 10390:1994 (E) protocol. Finally, we used spatial bilinear interpolation (based on *x* and *y*) to estimate soil pH values for the remaining plots. We forced the interpolated pH values between the range of the pH values of a given grid.

Freezing degree days (FDDs) and growing degree days (GDDs) were calculated from soil temperature, which was measured with miniature loggers (Thermochron iButton DS1921G and DS1922L). Temperature was logged at a 2–4 h interval for 1 year. We installed 72 loggers at the high-Arctic and at the low-Arctic sites (12 loggers per grid) and 378 loggers at the sub-Arctic site (18 loggers per grid). We installed them *c*. 10 cm below the soil surface. After 1 year of measurement, we had data from 69 loggers at the high-Arctic site (2018–2019), 72 at the low-Arctic site (2018–2019) and 322 at the sub-Arctic site (2013–2014). We used spatial bilinear interpolation to estimate soil temperature values for the remaining plots. We forced the interpolated temperature values between the range of the observed temperature values of a given grid. We averaged the soil temperatures to daily mean temperatures and used these to calculate FDDs and GDDs for each plot. FDDs are a sum of daily soil temperatures when temperature is below 0°C, which summarizes the harshness of winter thermal conditions to vegetation. GDDs are a thermal sum of days when mean temperature exceeds 3°C and thus accounts for both the overall amount of energy available for plants and the length of the growing season.

Organic layer depth was measured (in centimetres) using a thin metal rod. We measured ≤80 cm depth. We measured 72 plots at the high-Arctic and low-Arctic sites (12 plots per grid) and all the plots at the sub-Arctic site. We used bilinear interpolation to estimate organic layer depth values for the remaining plots at the high-Arctic and low-Arctic sites. We constrained the interpolated organic layer depth values between the range of the organic layer depth values of a given grid.

Solar radiation was represented by incident radiation, which was calculated as the maximum potential solar radiation (i.e., assuming clear sky conditions). In the calculations, we used the slope and aspect values that we measured *in situ* at each plot using rulers and a compass. We followed the methods of McCune & Keon (2002).

2.5 | Statistical methods

We assessed the collinearity of the environmental predictors using Spearman's correlation (Figure S3). We assessed the sites individually and the entire combined dataset (i.e., all sites together). The correlations were <.7, except for FDD and organic layer depth (.14 across all sites; .75 at the sub-Arctic site). FDD is a microclimate predictor that represents winter and snow conditions that can be more relevant to Arctic plants than summer thermal conditions (Niittynen et al., 2020). Organic layer depth represents the medium on which plants grow, and it is one of the most relevant predictors of spatial soil moisture conditions throughout the growing season (Kemppinen et al., 2018). Thus, it was important to include organic layer depth in the models, because our soil moisture measurements were snapshots. Despite their collinearity in the models, we decided to include both FDD and organic layer depth in further analyses, because they represent two important and completely different mechanisms that can help us to gain a better understanding of Arctic plant communities and their functional traits.

We used hierarchical generalized additive models (HGAMs) to analyse the data (Pedersen et al., 2019). For each of the seven plant traits, we fitted one multi-predictor HGAM. We fitted the HGAMs with the package MGCV v.1.8–31 (Wood, 2011). In the models, the effects of each environmental variable were represented by a thin plate spline constructed of 20 basis functions. Each model was built with four types of predictors. First, we included the "global" (data combined from three sites) trait–environment relationship for each environmental variable. Here, the "global" trait–environment relationship refers to a relationship that is transferable and generalizable within the three study sites (following methods and terminology of Pedersen et al., 2019). Second, we included the site-specific deviations from the "global" relationship as a factor-smooth interaction, in which all deviating splines share the same wiggliness. Third, we included a random intercept for each site-grid combination. Fourth, we included the site as a factor. We did not include the effect of sites as a random intercept because variance estimates for random intercepts of factors with only four levels are unreliable. The resulting model is a GAM equivalent of a linear mixed-effects model that has random intercepts for grids nested in sites and random slopes that vary by site, with the exception that the random intercepts for sites were fitted as factors. We used restricted maximum likelihood (REML) estimation to fit the models and specified that the smoothing parameters of the environmental response splines must have a value of at least one. We used R v.4.0.2. The marginal environmental responses of this model are presented in Figure 2. Site-specific response curves were acquired by summing together global and site-specific splines. Standard deviations for the site-specific response curves were acquired by summing the variances of the

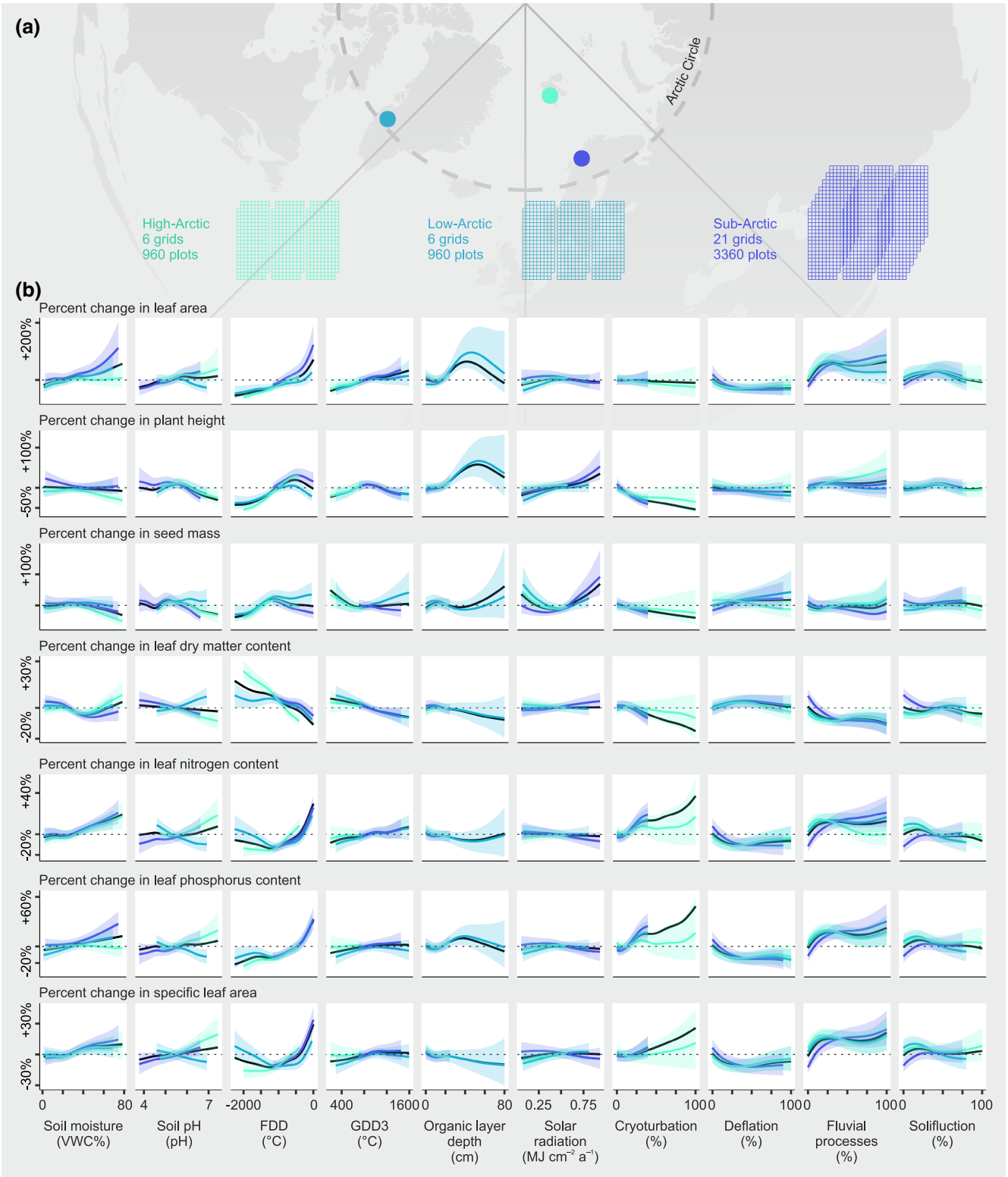

FIGURE 2 Consistent plant functional trait–geomorphology relationships. (a) The study design of three study sites across the Arctic. (b) The black continuous line represents the spline for the trait–environment relationships across the three sites. The coloured continuous lines represent each site separately. The shaded areas represent two standard deviations for the spline, taking into account the uncertainty in the smoothers. The global splines have a reference value of zero at the mean value of the environmental variable across the dataset. Abbreviations: FDD, soil temperature-derived freezing degree days; GDD3, soil temperature-derived growing degree days

global and site-specific splines. Given that the CWMs were $\log_{10}$-transformed, the responses represent changes in average traits along environmental gradients on a proportional scale. To visualize this, the environmental response curves were transformed to a percentage scale, where the reference level of zero change corresponds to the value of the trait in average environmental conditions in an average site.

We visualized two exemplar traits, plant height and specific leaf area, in relationship to the environmental gradients (Figure 3). Based on the HGAMs, we plotted the responses of the two exemplar traits in relationship to all possible pairs between the environmental variables (i.e., geomorphological process + microclimate or soil properties), which resulted in 24 plots of two-dimensional response surfaces per trait. The surfaces demonstrate how data points are distributed across these environmental spaces. This was used to explore more closely how the traits vary depending on two environmental variables at a time. The HGAMs fitted to the whole dataset with the same model structure presented above were used to predict plant height and specific leaf area for an artificial dataset. This dataset was constructed to range across all possible combinations of each pair (geomorphological process + microclimate or soil properties), while all other predictors were set to their median values, which were calculated based on all plots in the original dataset. To prevent predictions too far from the environmental space used in model fitting (i.e., extrapolation), we excluded data points in the artificial dataset that were further than 10% of the variable-specific range from the true observations. In model prediction, we excluded the site-specific smoothers and random intercepts. Thus, visualized environmental spaces focus only on the "global effects" of the predictors.

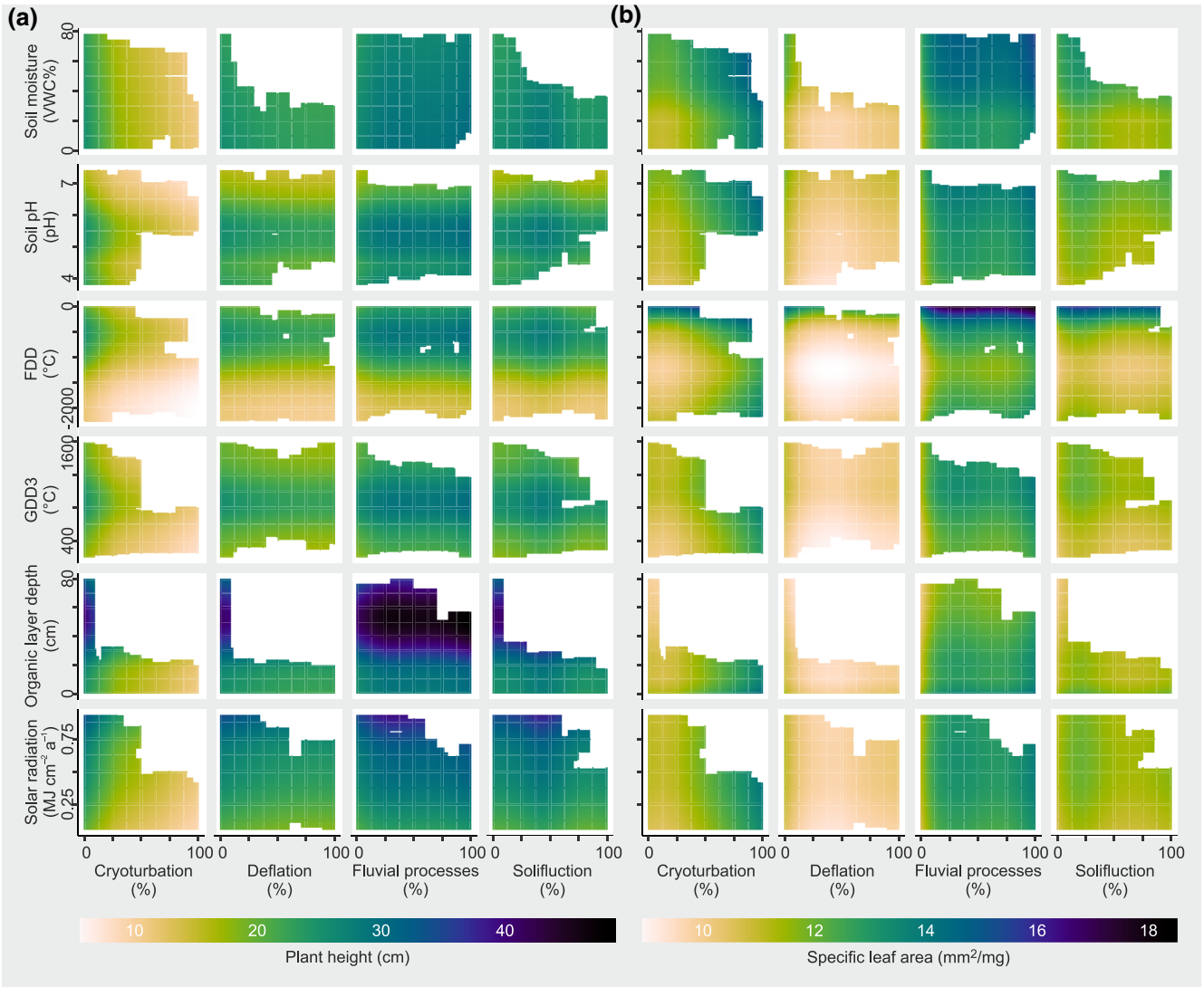

FIGURE 3 Plant functional traits in relationship to observed environmental gradients. (a) Plant height values were particularly low where cryoturbation was present. (b) Specific leaf area values were particularly high in habitats where fluvial processes were present and low where deflation was present. White represents parts of the gradient that are beyond the observed data. Abbreviations: FDD, soil temperature-derived freezing degree days; GDD3, soil temperature-derived growing degree days

We visualized the two exemplar traits spatially in relationship to possible changes in the four geomorphological processes (Figure 4). This analysis is based on the full dataset of the field observations, in which we simulated changes to the observed values for a given geomorphological process as follows. Initially, we created four simulated datasets for each process individually, while keeping the rest of the dataset unaltered. Then, in each dataset, we increased or decreased the percentage coverage of a given process by 50 or 100%. The 100% decrease is equivalent to removing the process entirely from the plot in which it was present. The 100% increase is equivalent to doubling the coverage of the given processes when present (up to a maximum of 100%). Then, we used the two example traits and their HGAMs to predict the traits into the simulated datasets. We did not alter the rest of the environmental predictors. Finally, we selected example grids, in which a given process was present while other processes were not, to visualize the sensitivity of the traits against changes in a given process.

3 | RESULTS

Our results revealed consistent trait–geomorphology relationships across the three Arctic sites (Figure 2; Table S3). This indicates that the relationships were more strongly determined by general trait–geomorphology relationships than by site-specific deviations from this global pattern (Figure 2). Overall, trait responses to each geomorphological process differed, indicating that each process has a unique influence on plant functional traits.

The analysis on two exemplar traits indicated that in plots with less cryoturbation (*c.* <25%), plants were taller than in more cryoturbated plots, regardless of the other environmental conditions (i.e., microclimate and soil variables; Figure 3a). This was not detected regarding deflation, fluvial processes or solifluction. Specific leaf area varied along the cryoturbation and fluvial processes gradients regardless of the other environmental variables (Figure 3b). This was not as evident regarding deflation or solifluction.

The visualizations of model simulations indicated that the height of plants increases if cryoturbation or deflation decreases (Figure 4a,c). Plant height decreases if cryoturbation or deflation increases (Figure 4a,c) or if fluvial processes or solifluction decreases (Figure 4e,g). Specific leaf area increases if cryoturbation, fluvial processes or solifluction increases (Figure 4b,f,h) or if deflation decreases (Figure 4d). Specific leaf area decreases if cryoturbation, fluvial processes or solifluction decreases (Figure 4b,f,h) or if deflation increases (Figure 4d).

4 | DISCUSSION

Here, we unveiled plant functional trait–geomorphology relationships across three distinct study sites in the Arctic tundra. We found that trait–geomorphology relationships are consistent across the sites, and that responses of structural traits and leaf economic traits to geomorphological processes contrast strongly (Figure 2). In many cases, the community traits are driven predominantly by these processes (Figure 3). This means that the trait responses to geomorphological processes are strong enough to mask the effects of variation in other environmental variables, and in turn, that these processes are important local-scale drivers of vegetation structure. Our correlative methods do not prove causation, but our observational approach provides missing insights into trait–geomorphology relationships in Arctic ecosystems. Our results from the Arctic (Figure 5), together with existing literature from alpine ecosystems (Apple et al., 2019; Kopanina et al., 2020), provide evidence for the importance of geomorphological processes in trait ecology.

4.1 | Trait responses to geomorphological processes

The four geomorphological processes that were present in our study grids across all three study sites are typical active agents of Earth surface systems across Arctic landscapes and are ultimately driven by different factors (temperature, wind, precipitation, snow and gravity) (Brook, 2018; French, 2017). In turn, each of the processes has a different effect on Arctic plant communities (le Roux & Luoto, 2014; Virtanen et al., 2010). In various ways, these geomorphological processes increase instability in the soil by relocating soil material (Brook, 2018; French, 2017), which might lead to altered soil nutrient availability and cause physical damage to the plants. These processes have strong effects on species composition (Giaccone et al., 2019; le Roux, Virtanen, et al., 2013), and now we report effects also on plant functional traits.

The trait–cryoturbation relationships were consistent across the three sites and revealed contrasting responses between structural and leaf economic traits. Our results indicate that at locations with high cryoturbation, plants grow smaller and have smaller leaves and seeds, while their leaf nutrient contents and specific leaf area increase. Focusing on plant height and specific leaf area, we noticed that both traits responded to possible changes in cryoturbation, except that specific leaf area showed almost no response to lower cryoturbation. We expect that these results can be explained by how cryoturbation mixes and relocates soil material (Ping et al., 1998). In turn, cryoturbation can foster both physical and chemical weathering and nutrient supply by exposing mineral soil material (Walker et al., 2004). In addition, the influence of cryoturbation can potentially be explained also by biotic interactions: taller plants shade smaller plants, which might restrict the small plants to less favourable habitats influenced, for instance, by cryoturbation (Niittynen & Luoto, 2018). Therefore, greater cryoturbation could have an additional positive influence on specific leaf area via competition.

The trait–deflation relationships indicated that both structural and leaf economic traits respond already to low levels of deflation, but that further increases in deflation have minimal effect on the traits. This was a consistent pattern across the study sites, except for seed mass, which was related negatively to deflation in the high-Arctic site, but

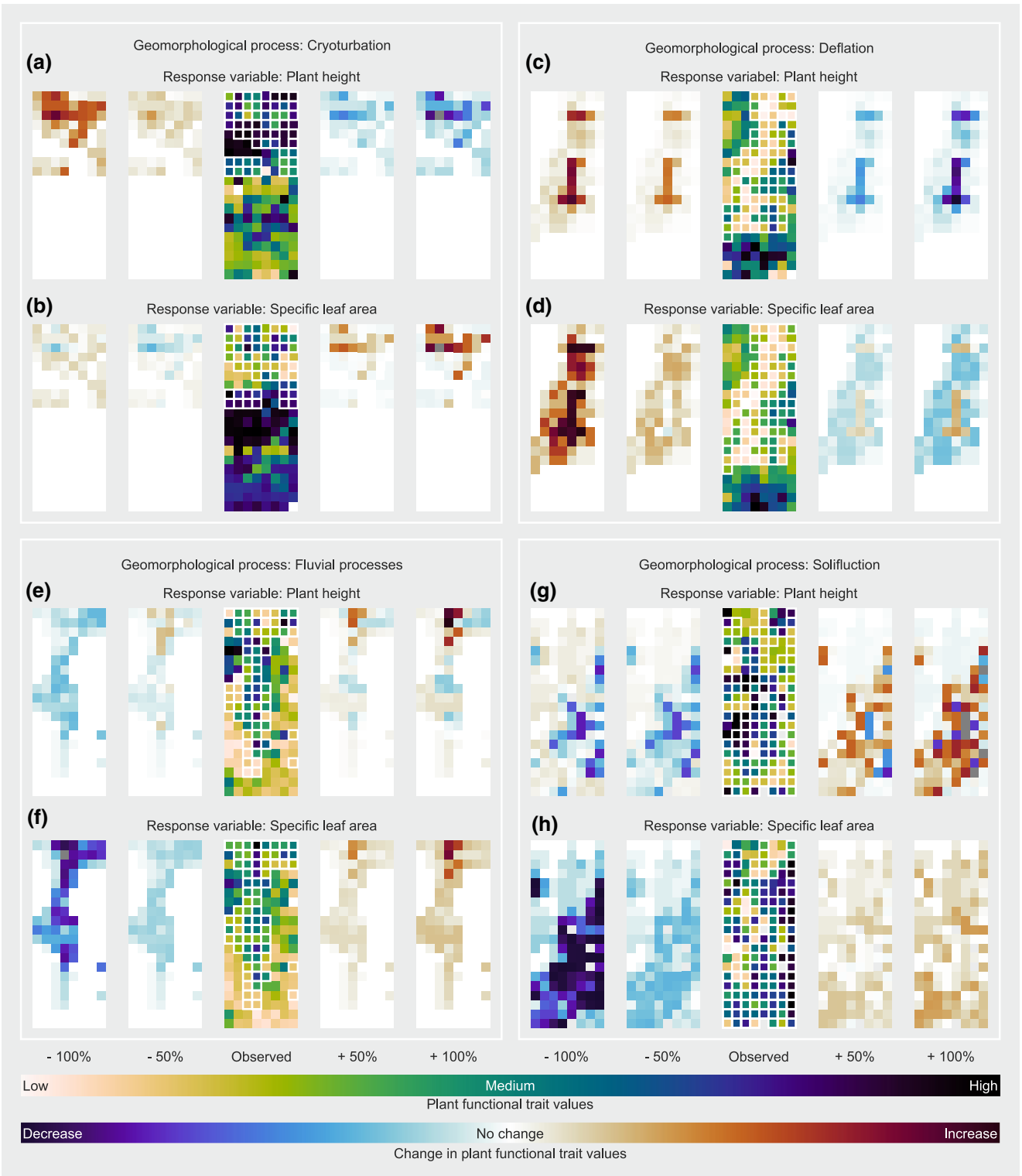

FIGURE 4 Plant functional traits in relationship to changes in the cover of geomorphological processes. For each geomorphological process, an example grid (8 m × 20 m) is presented here. Cells with white borders represent study plots in which a given process was observed to be present (coverage 1–100%). For instance, the grid in panels (a) and (b) is a study grid at the high-Arctic site in Svalbard, and in that grid only cryoturbation was present in the white-bordered plots, whereas other geomorphological processes (namely, deflation, fluvial processes and solifluction) were absent. The middle panel with the yellow–blue gradient presents the observed community-weighted mean plant height (a,c,e,g) and specific leaf area (b,d,f,h). The changes in plant functional traits represent outcomes of the hierarchical generalized additive models, which are predicted to manipulated data where a given geomorphological process has been increased or decreased by 50 or 100% in each plot. For instance, (a) plant height responds to changes in cryoturbation, and (b) specific leaf area responds to the decrease of cryoturbation (g,h)

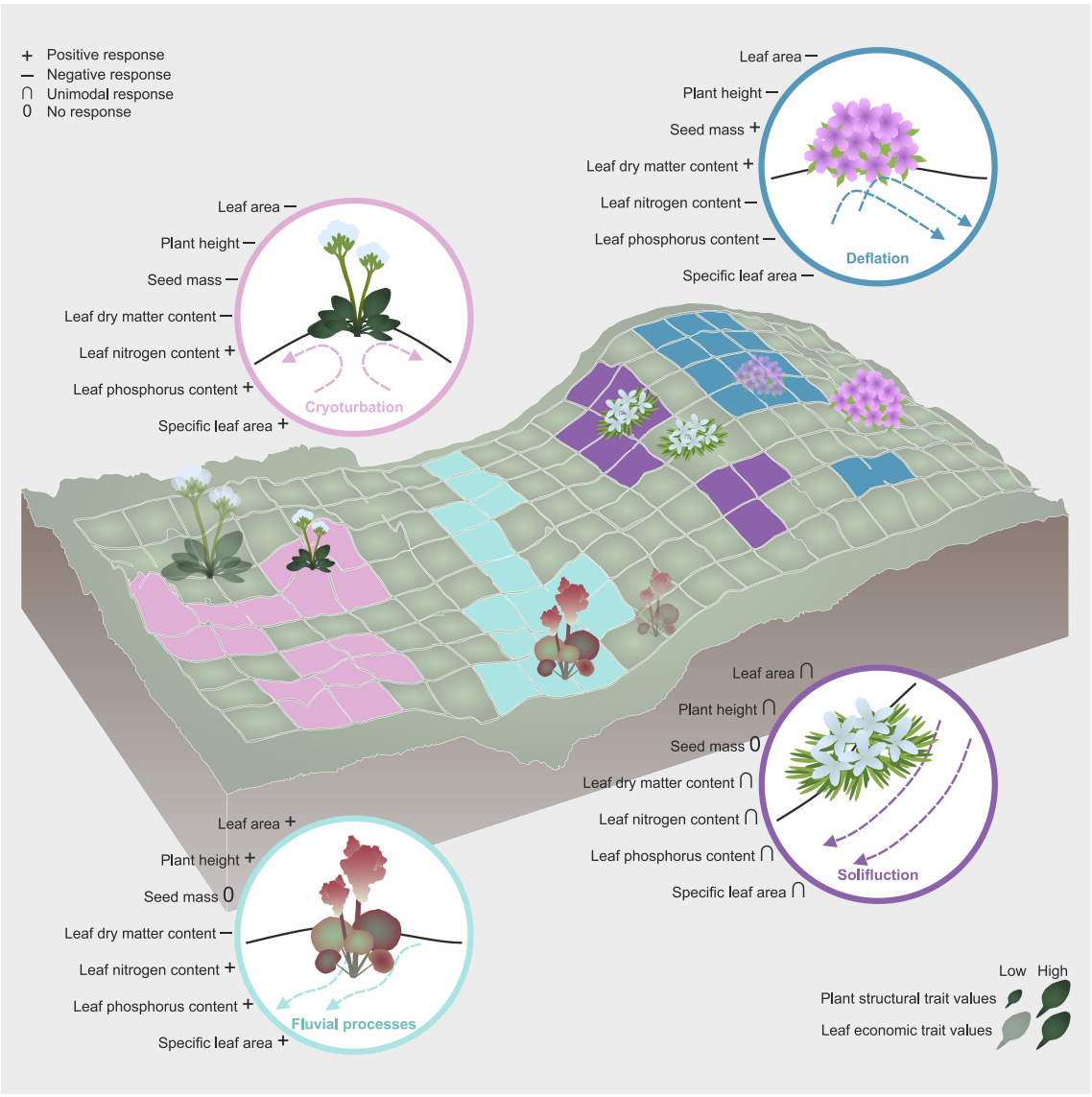

FIGURE 5 A summary of the results: Plant functional trait–geomorphology relationships in the Arctic

positively at the two other sites. We suspect that the inconsistent patterns related to seed mass can be explained, in part, by a few species that have especially large seeds (e.g., *Empetrum nigrum* and *Arctous alpina*) and that were not present at the high-Arctic site. When examining the responses of plant height and specific leaf area to deflation, both traits responded to possible changes in deflation; however, decreasing deflation had a stronger effect on specific leaf area than an increase. This is likely to reflect how deflation transports away both organic and fine soil material (which increases soil desiccation further) and causes physical disturbance to plants (Bridges & Laity, 2013; Wolfe, 2013). Consequently, deflation might decrease soil nutrient availability, which favours a conservative use of resources.

The trait–fluvial processes relationships were generally opposite to the trait–deflation relationships. The traits responded to low levels of fluvial processes, and further increases had minimal impacts on the traits. The three sites had similar responses, except for one of the seven traits: leaf nitrogen content had a unimodal response in the high-Arctic site. Both plant height and specific leaf area responded to possible changes in fluvial processes, and plant height had both positive and negative responses to increases in fluvial processes. We suspect that these results can be explained by how fluvial processes relocate fine sediments and increase seasonal variation of soil moisture, and overall, how they are related to other environmental conditions, such as winter conditions (snow cover duration, snow melt timing and duration of the snow melt period) and the formation of organic soils (Blankinship et al., 2014; Bring et al., 2016; Giblin et al., 1991). Consequently, the transportation and accumulation of water and soil, and in turn, the increase in relocation of nutrients and plant available water might favour both plant growth and the rapid use of resources.

The trait–solifluction relationships demonstrated that structural traits showed an approximately hump-shaped relationship with solifluction, in agreement with previous literature investigating the effect of this process on vegetation abundance (Hjort et al., 2014). Our results indicated that both structural and leaf economic traits

responded positively to increases across low levels of solifluction, whereas further increases had negative responses. This was the general pattern across the three sites. Both plant height and specific leaf area responded to possible changes in solifluction, and these results supported the unimodal response of plant height: if solifluction increases, plant height would decrease in some plots but increase in others. We believe that these results can be explained by how solifluction operates, which is by mixing and relocating soil material (Matsuoka, 2001). Consequently, low levels of solifluction (slow soil movement) would increase soil nutrient availability and favour the rapid use of resources without disturbing plant growth, whereas high levels of solifluction would be a disturbance to plant growth by destabilizing the soil (Ridefelt et al., 2011). This is because the depth of soil movement associated with solifluction can be deeper than the rooting depth of the plants, which can enable vegetation to grow on active solifluction sites. Nevertheless, it should be noted that in comparison to the other geomorphological processes investigated here, the effect of solifluction was negligible and clearly the weakest trait–geomorphology relationship.

4.2 | Future perspectives

In the tundra, disturbance ecology has long traditions of investigating plant communities in relationship to natural disturbances. Plant communities can, for instance, experience disturbance caused by geomorphological processes (Johnson & Billings, 1962), such as rapid mass wasting (landslides and rockslides) (Macias-Fauria & Johnson, 2013). In addition to these catastrophic events (short duration, high intensity), over time, geomorphological processes also sculpt the Arctic landscapes and provide a range of habitats by altering soil resources and stability (long duration, low intensity) (French, 2017). Our results highlight why geomorphological processes are not only a mechanical disturbance for vegetation, but how they also profoundly shape functional traits of the Arctic plant communities. Thus, it is important to consider and describe in detail whether and what type of disturbance geomorphological processes pose to plants and to determine the spatial and temporal extents and the overall intensity of the given disturbance (Graham et al., 2021).

As it becomes warmer in the Arctic, plants grow taller and cryogenic processes decrease (Aalto et al., 2017; Bjorkman, Myers-Smith, Elmendorf, Normand, Rüger, et al., 2018). Our results indicate that if cryogenic processes were completely lost, plant height would increase further, but specific leaf area would decrease. However, indirect effects and feedbacks across macroclimate, microclimate, geomorphological processes (and overall geodiversity) and Arctic biota can make the causal hierarchy complex, and it should be investigated thoroughly (e.g., via structural equation modelling). For instance, plants also shape geomorphology (Stallins, 2006; Viles, 2020); for instance, the expansion of woody plant species can reduce permafrost thaw (Blok et al., 2010; Nauta et al., 2015). At our study sites, woodiness of the plant community was reflected well by the functional traits (data not shown). For instance, leaf dry mass content had a strong positive correlation with CWM woodiness, whereas leaf area and plant height had a negative correlation. In future studies, it would be important to quantify the possible feedbacks of the trait–geomorphology relationships, especially in relationship to shrubification, particularly the differences between tall deciduous shrub communities and evergreen dwarf shrub communities (Vowles & Björk, 2019). Overall, geomorphology alongside plant ecology increases our understanding of trait–environment relationships in the rapidly changing Arctic.

4.3 | Conclusions

Here, we have shown that geomorphological processes shape plant functional traits in the Arctic. Previously, analyses on species composition have shown that geomorphological processes impact vegetation. Focusing on functional traits allows us to generalize results across sites with potentially dissimilar species compositions and reveals that the nature of geomorphological impacts is consistent across sites separated by thousands of kilometres. We, therefore, provide empirical evidence for the existence of generalizable relationships between plant functional traits and geomorphological patterns, and the results indicate that the relationships are universal across three distinct Arctic tundra ecosystems. This knowledge is important for improving the biological basis for predictions of climate change impacts over vulnerable Arctic ecosystems facing rapid shifts in both their biotic and abiotic environments.

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CONFLICT OF INTEREST

Authors have no conflict of interests.

AUTHOR CONTRIBUTIONS

J.K. conceived the research. J.K., P.N., P.C.I.R., J.A. and M.L. performed the field research. H.R. performed the laboratory analyses. J.K., P.N. and K.H. analysed the data. J.K. wrote the first draft. All authors edited the draft.

DATA AVAILABILITY STATEMENT

Data and code are openly available (Kemppinen et al., 2022; https://doi.org/10.5281/zenodo.6410638).

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BIOSKETCH

Julia Kemppinen is a postdoctoral researcher investigating global change in northern environments. All authors share an interest in understanding the spatio-temporal patterns of biotic responses to abiotic heterogeneity.

SUPPORTING INFORMATION

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APPENDIX A: DATA SOURCES

A.1 | Full citation list of the trait data.

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