Plant community borealization in the Arctic is driven by boreal-tundra boundary species

Running title: Tundra plant borealization

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Abstract

Following rapid climate change across the Arctic, tundra plant communities are experiencing extensive compositional shifts. One of the most prevalent changes is the encroachment of boreal species into the tundra (‘borealization’). Borealization has been reported at individual sites, but has not been systematically quantified across the tundra biome. Here, we use a dataset of 1,137 plots at 113 subsites across 32 study areas resurveyed at least once between 1981 and 2023 and encompassing 287 vascular plant species. We i) quantified the borealization of tundra ecosystems as the colonisation and the increase in abundance of boreal specialist and boreal-tundra boundary species, ii) assessed biogeographical, climatic and local drivers of borealization, and iii) identified species contributing most to borealization and their associated traits. Around half of the plots experienced borealization, especially at sites closer to the treeline, at higher elevations (mountains), in warmer and wetter regions, and at sites that had undergone the lowest magnitude of climate change. Boreal species were more likely to expand in Eurasia, and at sites with lower initial abundances of boreal species. Boreal species that colonised more plots were generally short, and more likely to be shrubs and graminoids than forbs. Boreal specialist species colonised three times less frequently than boreal-tundra boundary species, yet abundance changes were similar across groups. These findings indicate that borealization is mainly driven by the spread of already established species in the tundra, and suggest that future changes to Arctic ecosystems might not involve rapid, widespread replacement of Arctic species by boreal species. These observed and future plant community composition changes could affect land-atmosphere interactions, trophic dynamics and local and Indigenous livelihoods.

Introduction

Climate change is leading to widespread vegetation change in tundra regions (Myers-Smith et al. 2011; Elmendorf et al. 2012; García Criado et al. 2023a). Extensive changes to plant community composition have occurred, including changes in plant abundance and species range shifts (Elmendorf et al. 2012; García Criado et al. 2020) and treeline advance (Harsch et al. 2009; Frost and Epstein 2014; Rees et al. 2020). In this context, a conservation concern is that these shifts may include extensive encroachment of boreal species into the tundra ('borealization'; Speed et al. 2021). While borealization has been extensively studied in the marine realm (Fossheim et al. 2015; Pecuchet et al. 2020; Emblemsvåg et al. 2022), terrestrial studies are lagging far behind (Verdonen et al. in prep). Within the tundra, range expansions of boreal animals such as red fox (*Vulpes vulpes*), moose (*Alces alces*) and songbirds have been reported (Tape et al. 2016; Elmhagen et al. 2017; Le Pogam et al. 2021), and recent modelling shows northward movement of boreal herbivore communities as a result of warming temperatures (Speed et al. 2021). Despite some site-specific studies in Russia, Alaska and Canada (Khitun et al. 2016; Roland et al. 2021; Timoney 2023), the extent to which plant borealization (beyond treeline advance) is occurring at the tundra biome scale remains unquantified.

Borealization is likely to be dependent on a combination of geographic, climatic and local factors. Sites closest to the tundra-boreal forest ecotone might be more likely to experience successful plant dispersal and establishment from the boreal forest (Ropars and Boudreau 2012), especially those with no dispersal barriers such as large water bodies or mountain ranges (Rupp et al. 2001). Similarly, warmer conditions could favour boreal species as they inhabit a warmer thermal niche than tundra species (Villén-Peréz et al. 2020; Lynn et al. 2021). This could result in regional differences in borealization, since for example Arctic Europe (Palaearctic) is generally warmer than Arctic North America (Nearctic) and other regions (Callaghan et al. 2004a). However, local conditions can influence the establishment of boreal species into the tundra (Dial et al. 2022), with herbivory potentially preventing further plant colonisations (Eskelinen et al. 2017) and landscape structure driving adaptation and dispersal (Graae et al. 2018). Therefore, we could expect borealization to be shaped by a combination of factors acting from macro- to micro- scales.

Certain species might contribute to borealization more than others. For instance, species with large distributional ranges usually have a wider tolerance for environmental conditions (Vincent et al. 2020; Lynn et al. 2021) and are more likely to expand across tundra habitats (Callaghan et al. 2004b). Similarly, more competitive species such as shrubs, and species with great dispersal potential and/or fast acquisition strategies (Aubin et al. 2016) could have greater geographic and climatic niches (Sporbert et al. 2021) and thus become more successful tundra colonisers. Hence, plant trait values such as tall height, high specific leaf area (SLA), low seed mass or low leaf nitrogen concentration might be linked to successful borealization (Vuorinen et al. 2017; García Criado et al. 2023b). Incoming species can re-shape community traits, such as tundra plant communities becoming taller as a result of species turnover (Bjorkman et al. 2018a). Boreal species are generally taller than tundra plants, and might outcompete them through shading, higher litter production, and enhanced nutrient uptake (Pajunen et al. 2011; Kaarlejärvi et al. 2017; Thomas et al. 2020). Thus, the trait composition of tundra plant communities is likely to shift as boreal species become more abundant.

An influx of boreal species into the tundra will inevitably lead to changes in community composition, resulting in the widening or displacement of the boreal forest-tundra ecotone, a reduction of the tundra biome, or alternatively the creation of novel communities (Macias-Fauria et al. 2012). The boreal forest and the Arctic tundra are distinct in terms of ecosystem functioning and service provisioning, and a loss of extent of the tundra biome would have global consequences (Callaghan et al. 2002). For example, a northward advance of the forest-tundra ecotone has been projected to decrease carbon capture and amplify climate change (Zhang et al. 2013). A reduction in the extent of tundra can also result in decreased habitat availability for tundra herbivores (Speed et al. 2021), and cascading impacts for trophic chains (Fauchald et al. 2017; Mallory and Boyce 2018) and local and Indigenous communities (Rees et al. 2008; Hupp et al. 2015).

Here, we quantify borealization of plant communities across multiple tundra sites at the community and species levels over the past four decades, and address the following research questions (RQs):

RQ1. How much borealization has occurred across the tundra biome?

We expect that the majority of sites will have experienced an increase in boreal species presence and abundance, based on evidence from select intensively studied sites to date (Khitun et al. 2016; Roland et al. 2021; Timoney 2023).

RQ2. What are the characteristics of sites that have experienced the most pronounced borealization?

We hypothesise that borealization has been greater at sites closer to the treeline, at warmer sites, and where summer warming has been more pronounced, with thermal niches becoming available for warm-adapted species (Elmendorf et al. 2015; Steinbauer et al. 2018). We expect the Palaearctic to experience greater borealization relative to other Arctic regions given higher overall growing season temperatures and closer proximity of boreal ecosystems (Callaghan et al. 2004a).

RQ3. Which species are more likely to drive the borealization of tundra plant communities and what are their traits?

We expect ubiquitous species to have expanded and colonised more often due to their wider tolerance and niche (Callaghan et al. 2004b; Lynn et al. 2021). Certain functional groups like shrubs and species such as mountain birch (*Betula pubescens*) might have high expansion and colonisation rates due to their high dispersal capacity (Myers-Smith et al. 2011; Behrend et al. 2024). We hypothesise that certain species traits associated with an acquisitive life strategy (e.g., high SLA), greater competitive ability (e.g., tall stature), greater dispersal ability (e.g., lighter seeds) and lower palatability for herbivores (e.g., low leaf nitrogen; Aubin et al. 2016; Sporbert et al. 2021) will be associated with borealization.

Methods

Plant composition data

We extracted plant composition data from the database of the International Tundra Experiment (ITEX+; Bjorkman et al. in prep., Henry and Molau 1997), a geographically distributed experiment with a standardised study design and data collection. ITEX+ has a hierarchical structure, where each study area can contain several subsites, consisting of several sampling plots (Bjorkman et al. in prep). We selected ITEX+ study areas included within the boreal forest and tundra biomes according to the WWF ecoregions (Olson et al. 2001), which included Oro-Arctic (near-Arctic alpine sites), sub-Arctic and Arctic sites. We used only permanently-marked control plots (i.e., with no experimental treatments) that had been surveyed at least twice over a minimum of five years, as shorter time series can overestimate trends in tundra plant communities due to interannual variability (Harris et al. 2022; Valdez et al. 2023). Our dataset consisted of 33,388 records from 1,137 plots within 113 subsites in 32 study areas surveyed at least twice between 1981 and 2023, encompassing 287 vascular plant species. There was an average of 10 plots per subsite (range = 1-83), 3.5 subsites per study area (range = 1-31) and 15 years between samplings (range = 5-28). Our replication unit for analyses was a plot, with an average size of 3.86 m^2 (range = 0.05 - 120).

We followed the same method as in García Criado et al. (2023a) to convert vascular plant abundance values to relative cover (0 - 100%) within each plot in order to ensure consistency across survey methods (i.e., point-intercept data and cover-equivalent data). We retained only vascular plants since non-vascular plants are not recorded consistently across the ITEX+ dataset, and removed abiotic records prior to cover calculations. To standardise survey effort across sites, we removed plot-by-year combinations that reported >10% morphospecies (i.e., plants not identified to species level). We standardised the taxonomy of all species within the dataset following WorldFlora Online as of October 2024 (WFO 2024). Specifically, we matched species names in our dataset with those in WFO via the ‘WorldFlora’ R package (Kindt 2020) and aggregated subspecies and varieties to species.

Species classification

While there are different methods to categorise species according to their distributional range, we followed a standardised approach for consistency across species and regions. We followed the Arctic Biodiversity Assessment (Meltofte 2013) to classify vascular plant species. In particular, we followed Appendix 9.1 (Daniëls et al. 2013), which lists all Arctic vascular plant species and their distribution in the five Arctic subzones based on Elven (2007). We created groupings with all possible combinations of distribution and frequency across the Arctic and boreal zones (see **Table S1** for a detailed classification). We considered a species to be present in a particular zone when it was reported as 'scattered' or 'frequent' in Daniëls et al. (2013); in contrast, we considered a species to be absent in a particular zone if it was described as 'rare', 'uncertain' or 'introduced' (**Table S1**). When several subspecies or varieties per species were listed in Daniëls et al. (2013), we standardised them at the species level by assigning the more frequent category for each zone. For the nine species in our dataset that were not included in Daniëls et al. (2013), we checked their distribution in the Global Biodiversity Information Facility (GBIF 2024) to manually assign them a class. Carrying out random checks of the Daniëls et al. (2013) classification against GBIF ranges resulted in comparable species classifications (not shown). Overall, we defined four classes based on species' geographical ranges with respect to Arctic boundaries (Walker et al. 2005; Elven 2007):

- **Boreal specialists:** species only found south of the tundra biome boundary, *n* = 16.
- **Boreal-tundra boundary:** species distributed in the boreal and Low Arctic tundra (subzones D-E), but not the High Arctic tundra (subzones A-C), *n* = 150.
- **Arctic specialists:** species found only north of the tundra biome boundary, *n* = 14.
- **Ubiquitous:** species found in the boreal zone, Low Arctic and High Arctic, *n* = 107.

Hereafter, we consider 'boreal' to include both boreal specialist species and species distributed across the biome boundary but not extending into the High Arctic (i.e., boreal-tundra boundary species). We consider boreal-tundra boundary species to contribute to borealization on the basis of their evolutionary history. In most cases, current species distributions in the boreal and Low Arctic zones are the result of expansions from boreal into Arctic locations that were previously glaciated (Birks 2008; Aarnes et al. 2012) and thus represent long-term borealization processes. Boreal-tundra boundary species could also include those that survived glaciations in refugia (Abbott et al. 2000), but these are very likely a minority compared to the former (Alsos et al. 2022).

Borealization indices

We assessed borealization in each plot (i.e., at the community level) both in terms of colonisations and abundance changes of boreal species. First, we defined the Borealization Colonisation Index (BCI; RQ1). This metric considers the start and end time points of monitoring per plot and reflects the extent of 'borealization' of a plot over time based on the influx of new boreal species. BCI reflects the proportion of colonisers that are boreal species (boreal specialists and boreal-tundra boundary species), and is bound between 0 and 1. This metric does not directly account for duration of monitoring, but we found no relationship between BCI and duration (slope = 0.001, CI = -0.017 to 0.018). BCI is calculated as follows:

$$BCI = \frac{Colonising\ boreal\ species}{Total\ colonising\ species}$$

To quantify borealization per plot based on changes in abundance of boreal species, we defined the Borealization Abundance Index (BAI; RQ1). This metric reflects how 'borealized' a plot has become over time, considering the values of relative cover of boreal species (boreal specialists and boreal-tundra boundary species) at the start and end time points of monitoring per plot. BAI quantifies the rate of change in proportional cover of boreal species per year per plot. BAI is expressed as a rate (% cover change per year) and can be positive or negative. BAI is calculated as follows, where *b* refers to boreal species:

$$BAI = \frac{(\Sigma b\ End\ cover\ -\ \Sigma b\ Start\ cover)}{Duration\ (years)}$$

We calculated both BCI and BAI as the difference between the end and start time points per plot rather than fitting linear models to calculate slopes for plots for which we had multiple observations over time. This is due to the fact that BCI is a colonisation index, thus the starting value would always be 0 (since there are no colonisers in the first time point). In practice, this means that the index could have a negative value due to fluctuations in the number of boreal colonisations over the years, and thus the end-start method gives a more accurate representation of colonisations. Since BAI had a strong correlation between the end-start method and linear models (Pearson's $r = 0.97$, $p < 0.001$), we opted for consistency by calculating both BCI and BAI in a similar manner.

Drivers of community-level borealization

We selected relevant drivers of community-level borealization reflecting main biogeographical (latitude, biome, distance to treeline, barriers to dispersal and biogeographic region), climatic (climatologies and climate change, see below) and local factors (herbivory intensity, dominant grazer, elevation, moisture, plot size, permafrost and initial abundance of boreal species).

For each subsite (i.e., the level at which geographic coordinates were available), we extracted latitude and biome (Oro-Arctic or Arctic) information, as defined in Olson et al., (2001). Additionally, we calculated the distance to the nearest treeline. For Arctic plots (those north of the latitudinal treeline), we calculated the distance to the latitudinal treeline from the Circumpolar Arctic Vegetation Map (Raynolds et al. 2019) on QGis (version 3.30.2), and for Oro-Arctic plots, we calculated the distance to the elevational forest line using satellite data on Google Earth (version 10.65.1.2). For Oro-Arctic plots, we corrected the distance to the elevational treeline to reflect the "ground distance" by calculating the hypotenuse, considering the elevation of the subsite and of the elevational forest line. Distance to treeline was centred on zero by subtracting the mean to allow for model convergence. We also categorised barriers to dispersal for each subsite based on the type of topographical features that were found between the subsite and the latitudinal (for Arctic plots) or elevational treeline (for Oro-Arctic plots) as: uninterrupted, small water body (e.g., lakes, rivers), mountains, and large water bodies (e.g., seas, oceans). We also categorised each plot by their biogeographic region, according to glaciation history (Ray and Adams 2001) into Eastern North America, Western North America, Greenland-Iceland and Eurasia.

We extracted climatic data from CHELSA v2.1 for each subsite for the time period 1980-2019 at a resolution of 1x1 km (Karger et al. 2017). We calculated both climatologies (average value per climatic variable over time) and change over time (as slopes of climate variables over the years) for the following climatic variables: summer temperature (mean of the June, July and August months, to reflect growing season conditions), minimum annual temperature (as the mean daily minimum air temperature, to reflect plants' capacity to withstand cold) and annual precipitation (to reflect comparative water availability). We removed climatic data for 1980-1983 mean annual temperature and for 2005 minimum temperature since the files contained obvious data errors. The value of precipitation change of 18.24mm per year at the INCLINE_SKJ subsite was removed, as it was a clear outlier. This high value is likely due to the quantification of climatic values in extremely rugged terrains including fjords and mountains, despite the high resolution of CHELSA at 1x1 km.

Finally, we included variables at the subsite level available in the ITEX+ dataset, as provided by the site principal investigators, relating to biotic interactions (herbivory intensity, dominant grazer), local environmental conditions (elevation, moisture) and sampling effort (plot size). We extracted permafrost data for each subsite from Obu et al., (2019) as the Permafrost Probability Function (100m pixel size), which was then converted into standardised categories (none, sporadic, discontinuous, continuous). Initial boreal status was calculated at the plot level as the number of boreal specialist and boreal-tundra boundary species present at the start of the plot monitoring period for BCI models, and as the total relative cover of boreal specialist and boreal-tundra boundary species at the start of the monitoring period for BAI models.

Species trait data

We extracted plant trait data from TRY v6.0 (Kattge et al. 2020), which includes trait values from multiple campaigns, including the Tundra Trait Team (Bjorkman et al. 2018b). For each species, we extracted georeferenced records found north of 50° latitude for plant height (m), specific leaf area (SLA; mm^2/mg), leaf nitrogen (mg/g), leaf C:N (g/g) and seed mass (mg). We also kept non-georeferenced trait data when it was evident from metadata that the records had been taken at locations north of 50° latitude. We retained data for those species that had a minimum of five records per trait. We removed 118 outlier records (i.e., the value was greater than five standard deviations of the mean trait value per species). The final dataset contained trait data for 191 species (plant height), 166 species (SLA), 83 species (seed mass), 120 species (leaf N) and 54 species (leaf C:N). We calculated the mean trait values for each species, which were then incorporated as fixed effects in the species-level models (see below). Additionally, we included the following categorical traits: woodiness, deciduousness, N-fixing capacity (by symbiosis with N_2-fixing bacteria), berry-production, taxonomic family and functional group (shrubs, forbs, graminoids). While certain shrubs in our dataset could potentially reach enough height to become a tree, particularly outside of the Arctic, we do not make a distinction between these and refer to them as shrubs.

Community-level models

To assess the drivers of community borealization, both for BCI and BAI, we fitted three Bayesian hierarchical models that reflected the effect of the different variables at different scales (RQ2; **Table S2**): 1) biogeographical model, 2) climatic model, and 3) local model. We also tried fitting a single model including all predictor variables of interest, but this model failed to converge.

In order to characterise plots with boreal expansions only (**Table S2**), we retained those plots whose average BCI or BAI was > 0; hereafter 'positive-only models'. The plots included in each dataset differ (BCI: *n* = 598 plots, BAI: *n* = 488 plots) because plots that had experienced boreal colonisations did not necessarily undergo increases in abundance of boreal species on average, and *vice versa*. To characterise the full gradient of change (**Table S2**), we also ran models with the same fixed effects including plots without boreal colonisers (i.e., plots with 0 values for BCI, *n* = 1,137) or plots with no change or reductions in abundance of boreal species (i.e., plots with negative and 0 values for BAI; *n* = 1,137), hereafter 'full-range models'. When plots never had boreal species at the start or at the end, or they had boreal species in between timepoints, but not at the start and/or end survey timepoints, they were assigned a BCI and/or BAI = 0 accordingly. We interpret the BCI 'positive-only' models to indicate the 'borealness' of the colonisers, while the 'full range' BCI models inform about both the likelihood of borealization occurring, and the 'borealness' of those colonisations. BAI 'positive only' models refer to the boreal abundance increases, while BAI 'full-range' models reflect the 'net borealization' of the community. Finally, to assess how well colonisations by boreal species represent net borealization of the plots (i.e., an increase in the representation of boreal species between the two timepoints), we calculated the net change per plot as the difference between boreal colonisations and boreal losses. We found that BCI and the net change values are positively correlated (**Figure S1a**), indicating that a high BCI value generally corresponds to a net increase in the number of boreal species in a plot.

Prior to building the models, we assessed pairwise correlations among all the potential predictor variables for each type of model (biogeographic, climatic and local) within the 'positive-only' dataset. Only complete pairwise observations were included, i.e., those plots that had data available for all predictor variables. We calculated Spearman's rank correlation indices between pairs of variables for the subsets of variables included in each of the three community-level models (**Figure S2**). Given that pairwise correlations can only be computed for continuous or ordinal data, we coded categorical variables as ordinal values (see **Figure S2**). For strongly correlated variables (absolute Spearman's rank coefficient > 0.7), we kept the variables that more closely aligned with suspected mechanisms of change, as per our hypotheses. In the biogeographical models, we removed latitude and barriers to dispersal, as they were strongly correlated with distance to treeline, which was our main hypothesis (**Figure S2a**). In the dataset for BAI, biome was also removed as it was strongly correlated with distance to treeline (**Figure S2b**). In the climatic models, we removed minimum temperature climatology, which was strongly correlated with precipitation climatology, and we only had one climatology variable related to precipitation but multiple related to temperature (**Figure S2c, d**). No predictor variables were removed from the local models (**Figure S2e, f**).

We employed a Bayesian framework for all analyses. All community models included subsite as a random effect to account for the ITEX nested sampling design. Models had different error distributions depending on the structure of the response variable: Gaussian with an identity link function (for response metrics with a normal distribution, e.g., BAI models), beta with a logit link function (for values between 0.0001 and 0.9999; e.g., the BCI positive-only models, subtracting a constant of 0.0001 for BCI to fit the data into a beta distribution), and binomial models with a logit link function for integer count values (e.g., the BCI full-range models with values between 0-1). Binomial models are used to model proportions where the response variable is a count of cases that can fall into only one of two classes (Dunn and Smyth 2018). Here, we used the binomial family to model BCI per plot as the count of boreal colonisers out of the total number of colonisers.

Species-level models

To assess which species and species classes are more likely to drive the borealization of tundra plant communities (RQ3), we calculated how many times each species had colonised different plots (i.e., times colonised, expressed as number of plots), and its average abundance change per year across all plots. We then modelled times colonised (only those species that had colonised at least once) and average abundance change (only those that had increased in abundance across plots) as a function of species class. As above, we calculated the net change per species as the difference between the number of plots colonised and the number of plots where the species became extinct. We found a positive correlation between times colonised and the net change per species (**Figure S1b**), indicating that more frequent colonisations per species generally correspond to a net increase across plots.

To identify which traits are associated with species contributing to borealization (boreal specialists and boreal-tundra boundary species), we retained those species that had colonised at least once (for colonisation models) and that had increased in abundance on average across plots (for abundance models). Then, we modelled times colonised and abundance change as a function of relevant plant traits (**Table S2**). Continuous traits were log-transformed as species differences are better characterised on a log-scale (Westoby 1998; Bjorkman et al. 2018a). Similar to the community-level models, we assessed pairwise correlations between traits using Spearman’s rank correlation indices for all trait variables (**Figure S3**). Categorical traits were transformed to ordinal variables for investigating correlations (**Figure S3**). We removed Leaf C:N from the species models, as this trait is inherently correlated with Leaf N (**Figure S3**), and Leaf N had a greater number of available records. Leaf C:N was also correlated with SLA and seed mass in the colonisation dataset. To enable model convergence, we chose not to include the following categorical variables: woodiness (because it is exclusively associated with shrubs, one of the categories of the ‘functional group’ variable), berry production (as there were only nine berry-producing shrubs), deciduousness (as there were only 27 deciduous shrubs and 16 evergreen shrubs, while this category was not applicable to the remaining 228 [83.8%] species), taxonomic family (since 11 [30.5%] family groups had just one species), and N-fixing capacity (since there were only 10 N-fixer species).

Since the trait model reduces sample size to those species with data for all traits (**Table S2**), we fitted additional univariate models to identify any potential differences when using a larger sample size. Species-level models had a negative binomial data distribution with a log link function (for count data where the variance is greater than the mean, e.g., the 'times colonised' models), and a Gaussian distribution with an identity link function (for response metrics with a normal distribution, e.g., the 'mean abundance change' models). We specified weakly informative priors for the dispersion parameter of the negative binomial family.

Further, to better understand the relationship between species-level gains and losses, we calculated the number of times that a species was lost from a plot ('times lost') and modelled its relationship with times colonised. Finally, to understand whether these traits were exclusively associated with colonisations or they reflected turnover dynamics through greater number of extinctions, we also modelled 'times lost' as a function of the different traits.

Software

We used the software and programming language R version 4.2.0 (R Core Team 2022). Bayesian models were fitted using the 'brms' package (Bürkner 2017). We ran four chains per model, each with 2,000 iterations, and 400 iterations of warm-up. Convergence was assessed through examination of the R_{hat} term and trace plots. Correlation plots were visualized with the 'corrplot' package (Wei and Simko 2021).

Results

Community analyses

Boreal species colonised 52.6% of plots, with strong variability in magnitude across plots (**Figure 1a, b**). When considering only plots that had experienced boreal colonisations (i.e., BCI > 0, *n* = 598), mean BCI across plots was 0.77 (range = 0.16 to 1). When including zero values (*n* = 1,137), mean BCI was 0.4 (range = 0 to 1; **Figure S4a, b**). Similarly, boreal species increased in abundance at 42.9% of plots, also with considerable variation across plots (**Figure 1c, d**). For plots with BAI > 0 (*n* = 488), mean BAI was 0.93% increase per year (range = 0.007 to 5.79). For the full range of values (i.e., 'net borealization; *n* = 1,137), mean BAI was -0.09% per year (range = –5.82 to 5.79%, CI = -0.2 to 0.1, **Figure S4c, d**).

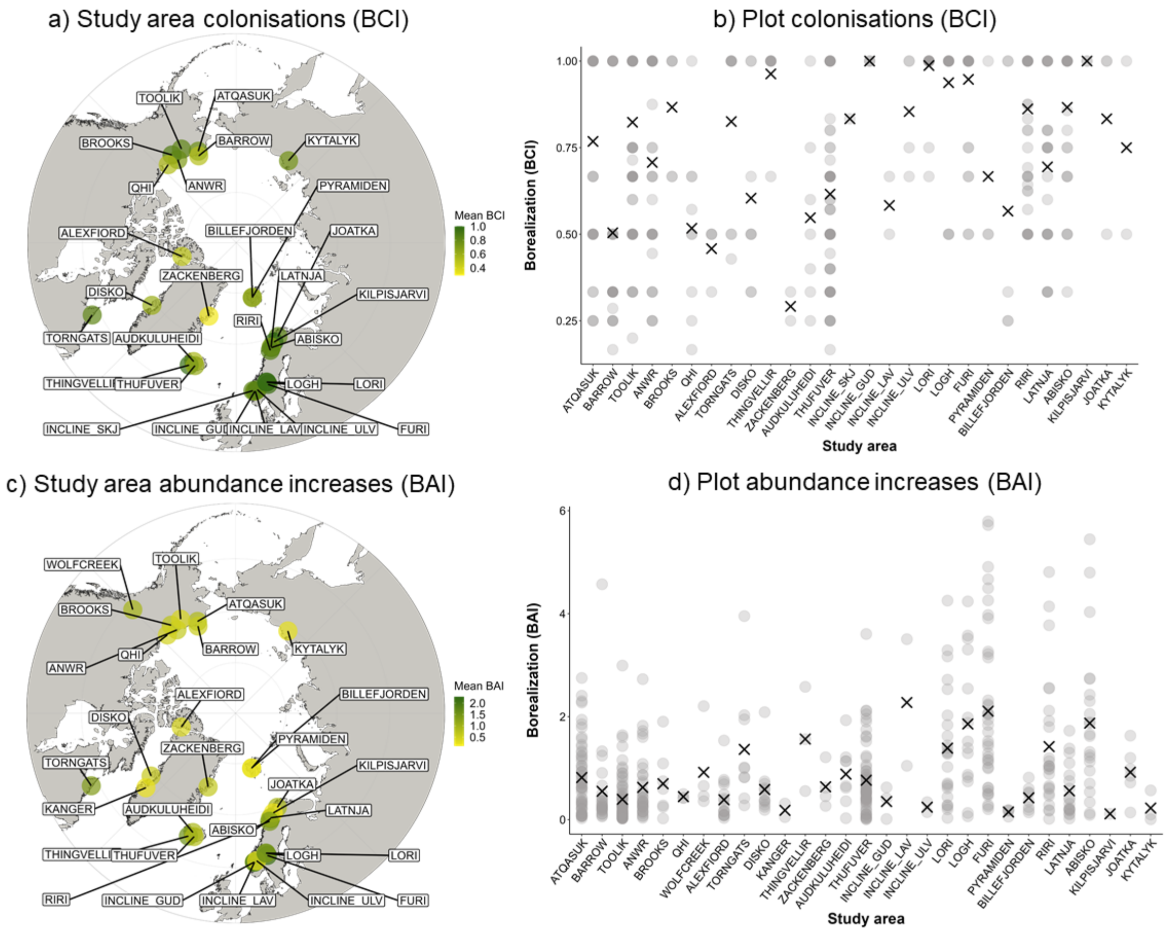

Figure 1. The magnitude of boreal plant community colonisations (BCI) and plot abundance increases (BAI) varied across the tundra. **a)** BCI estimated as the average of the plots within a study area that experienced colonisations of boreal species (BCI > 0), **b)** BCI index of those plots within each study area, **c)** BAI estimated as the average of the plots within a study area that experienced an increase in the abundance of boreal species (BAI > 0), **d)** BAI index for those plots within each study area. Points in **a)** and **c)** are coloured according to the magnitude of increase (as BAI and BCI) as a study area average. Crosses in **b)** and **d)** indicate the mean value of the plot borealization index at the study area level, which represent the same value as coloured points in **a)** and **c)**. Study areas in **b)** and **d)** are arranged by longitude. Darker grey colours indicate overlap of multiple points. Note that these data show the magnitude for plots that experienced increases in boreal species; for an analysis that includes plots where boreal increases did not occur (BCI = 0 and BAI <= 0), see **Figure S4**.

Within plots that had experienced boreal colonisations (i.e., 'positive-only' BCI models), these were greater at sites in Eurasia relative to Greenland-Iceland (**Figure 2a**), that were relatively warm (**Figure 2c**), had warmed least over time (**Figure 2e**) and increased least in precipitation (**Figure 2f**). When considering the 'full-range' BCI models (i.e., including zeroes), we found that boreal colonisers were more likely to occur closer to treeline (**Figure 2b**), in warmer and wetter sites (**Figure 2c, d**), at higher elevations (**Figure 2g**) and in larger plots (not shown; slope = 0.014, CI = 0.0051 to 0.0234).

The magnitudes of boreal abundance increases (i.e., ‘positive-only’ BAI models) were stronger in Eurasia compared to Western North America (**Figure 2h**), at sites closer to treeline (**Figure 2i**), that had increased least in precipitation (**Figure 2j**) and that had lower initial boreal abundance (**Figure 2l**). In the ‘full-range’ BAI models (i.e., including zeroes and negative values), net borealization was greater at higher elevations (**Figure 2i**) and where the initial abundance of boreal species was lower (**Figure 2l**). All other variables in the biogeographic, climatic and local models had credible intervals that overlapped zero.

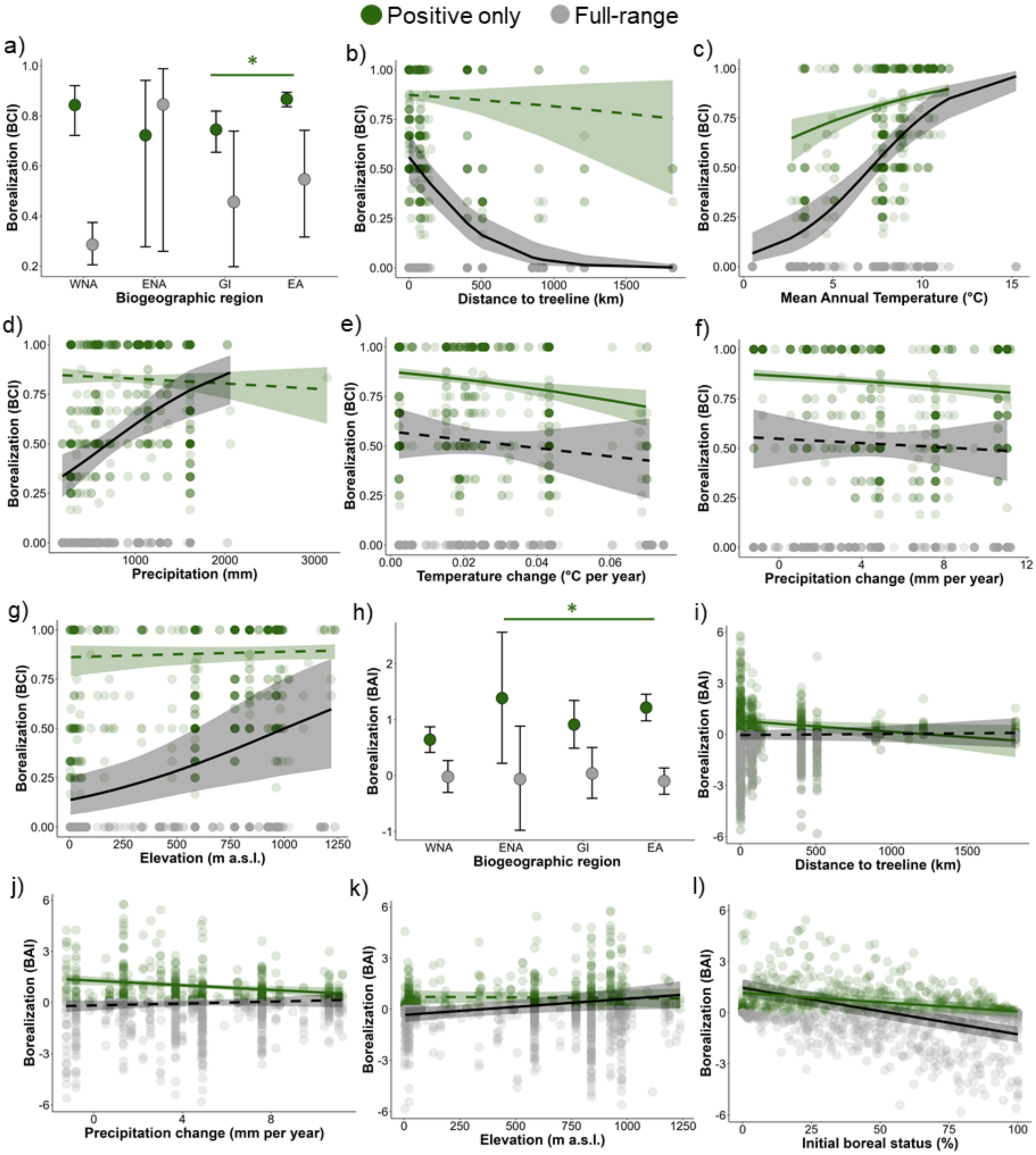

Figure 2. Borealization was associated with biogeographic, climatic and local variables across the tundra biome. Borealization was estimated using colonisations (BCI; **a-g**) and abundance change (BAI; **h-l**). Colonisations by boreal species were more likely to occur (i.e.,

‘full-range models’) at sites closer to the treeline (**b**), warmer and wetter sites (**c, d**) and at higher elevations (**g**), while greater magnitudes of boreal abundance increases (i.e., ‘positive-only models’) occurred at sites in Eurasia (EA) versus Greenland-Iceland (GI), while other regions overlapped (WNA = Western North America, ENA = Eastern North America; **a**), and at warmer sites (**c**) with the least amount of climate change (**e, f**). Increases in abundance of boreal species were more likely (i.e., ‘full-range models’) at higher elevations (**k**) and in plots with lower initial boreal status (**l**). The magnitudes of abundance increases (i.e., ‘positive-only models’) were stronger in Eurasia (EA) than in Western North America (WNA; **h**), at sites closer to treeline (**i**), that had experienced the least increases in precipitation (**j**) and that had lower initial boreal abundance (**l**). The panel shows all variables that were significant in at least one of the two models (i.e., ‘positive-only’ and ‘full-range’ models). Lines and semi-transparent ribbons represent the model estimate and 95% credible intervals, respectively, and are coloured according to model type (i.e., ‘positive-only’ in green and ‘full-range’ in grey). Solid lines indicate credible intervals of fixed effects that did not overlap zero, and dashed lines indicate credible intervals that overlapped zero. Each point represents a plot, with darker colours indicating point overlap. Green points are included in both the ‘positive-only’ dataset (i.e., positive values only, BCI: 598 plots, BAI: 488 plots) and in the ‘full-range’ dataset (i.e., including also zeroes and negative values, BCI and BAI: 1,137 plots). Grey points indicate plots only included in the ‘full-range’ dataset (i.e., zeroes and negative values), in addition to the positive values. Asterisks indicate when two categorical variables differed significantly from each other, coloured according to model type.

Species analyses

Overall, there were 3 and 3.3 times fewer colonisations of boreal specialists than boreal-tundra boundary and ubiquitous species, respectively (**Figure 3a**). However, the magnitude of species abundance increases did not differ across different classes (**Figure 3b**). The top coloniser species were the ubiquitous shrub *Empetrum nigrum* (72 times), the ubiquitous forb *Persicaria vivipara* (67 times) and the boreal-tundra boundary graminoid *Carex bigelowii* (62 times). Of all species colonising new plots, 64.4% were present within the subsite at the start of monitoring. The species that increased most in abundance include the boreal-tundra boundary shrub *Salix arctophila* (0.87% cover change per year), and the boreal-tundra boundary forbs *Galium verum* (0.83% cover change per year) and *Boykinia richardsonii* (0.77% cover change per year). Generally, species with greater increases in abundance were those that had colonised more frequently over time (slope = 0.75, CI = -0.02 to 1.52), but there was wide variation across species and rates (**Table S3**). Generally, species that were gained more frequently were also lost more often (slope = 0.66, CI = 0.59 to 0.72).

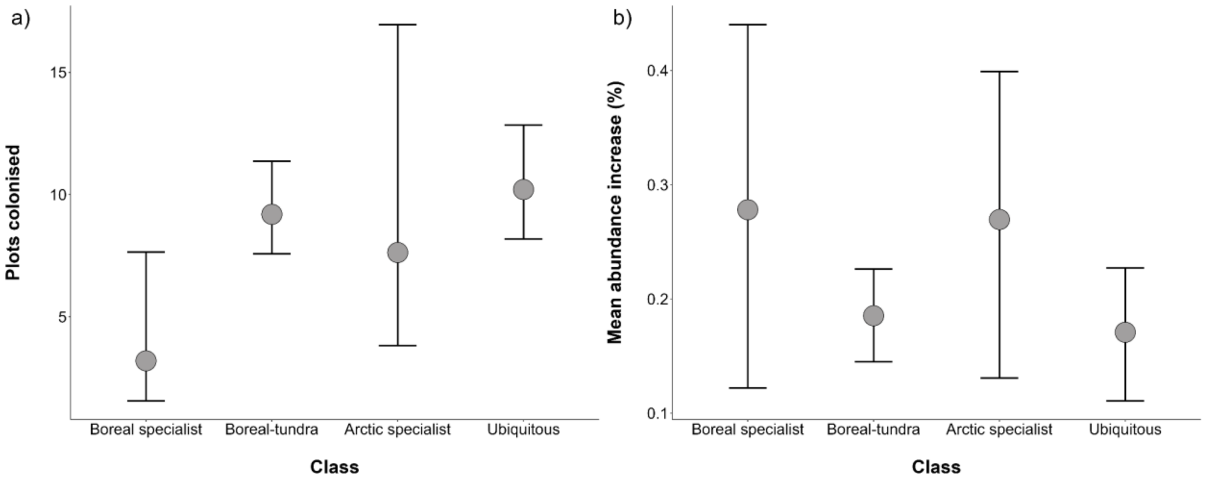

Figure 3. Model estimates at the species level, with **a)** total number of times colonising plots (model sample size = 220), and **b)** mean annual abundance increases across all plots (model sample size = 129), as a function of class. Points indicate the mean model estimate for each class, and error bars the 95% credible intervals. Sample sizes for categories in **a)** are: Boreal specialist = 9, Boreal-tundra boundary = 113, Arctic specialist = 9, Ubiquitous = 89 species. Sample sizes for categories in **b)** are: Boreal specialist = 5, Boreal-tundra boundary = 77, Arctic specialist = 7, Ubiquitous = 40 species.

Boreal species that colonised and increased in abundance were associated with different traits. Plant height influenced boreal colonisations: shorter species colonised more plots than taller species in the multivariate model (**Figure 4a**), although they were also likely to be lost from plots more often (slope = -0.72, CI = -1.18 to -0.25). Boreal graminoids and shrubs colonised 2.4 and 5.6 times more than forbs, respectively, in the multivariate model (**Figure 4b**), while in the univariate model only shrubs colonised more often than forbs (shrub estimate = 0.76, CI = 0.28 to 1.26). Graminoids and shrubs were also lost more frequently from plots (graminoid estimate = 1.97, CI = 1.11 to 2.87, shrub estimate = 2.57, CI = 1.36 to 3.90). There were no other significant traits associated with times colonised in the multivariate model, but in the univariate model species that colonised more often were associated with lower SLA (slope = -0.72, CI = -1.22 to -0.21). Species abundance increases were not associated with any of the five traits tested in either the multivariate or in the univariate models. Proportions of boreal coloniser and expanding species per functional group reflected those of the main dataset (i.e., including all species; *z*-tests, *p* = 0.26 for colonising species and *p* = 0.15 for increasing boreal abundance).

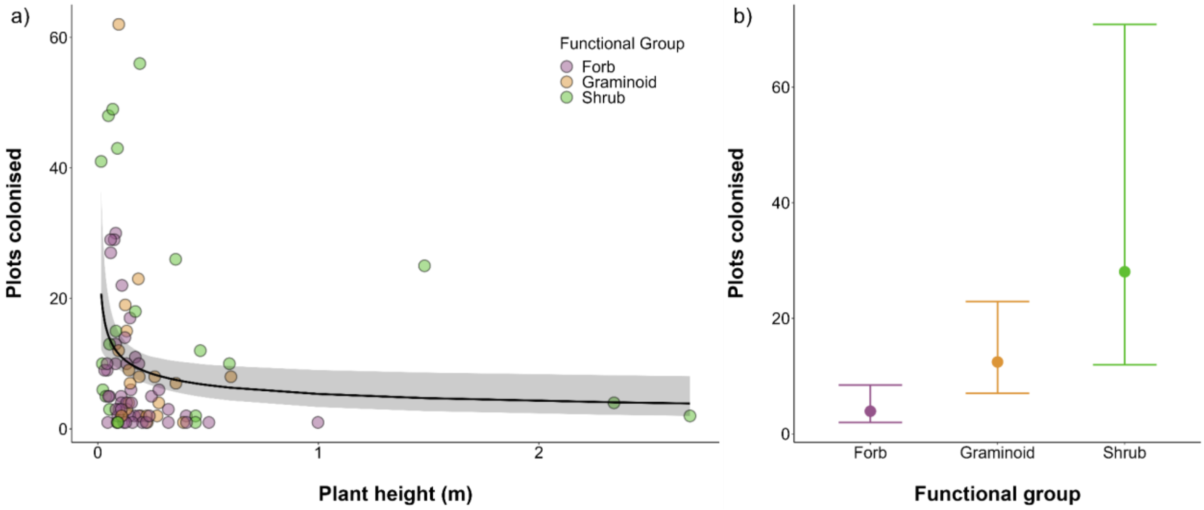

Figure 4. Colonising boreal species were shorter and more likely to be shrubs or graminoids, though shrub species spanned the full range of height values. **a)** Boreal species that were shorter colonised plots more often than taller species. Each point represents a plot, coloured according to the functional group. The line and ribbon represent the model estimate and 95% credible intervals of the univariate model (to allow for illustration of all the available height values). **b)** Boreal shrubs and graminoids colonised more often than forbs. Model outputs are represented as the mean estimate (points) and the 95% credible intervals (error bars). Sample sizes for each category in the model are: forb = 62, graminoid = 32, shrub = 28 species.

Discussion

While across all sites net borealization was limited, and 44.1% of plots experienced a decline in abundance of boreal species (**Figure S3**), our study shows that borealization occurred in around half of the studied plots, with 52.6% and 42.9% of plots experiencing colonisations by and increases in abundance of boreal species, respectively (**Figure 1**). These figures align closely with Harsch et al. (2009) and Rees et al. (2020), who reported treeline advance at 52% of studied sites, and forest-tundra ecotone advance at 52.3% of sites, respectively. Boreal expansions were more likely to occur closer to treeline, at warmer and wetter sites and at higher elevations (BCI), and at higher elevation sites that had lower initial abundance of boreal species (BAI). Within plots with positive rates, boreal increases were greatest at warmer sites (BCI) that had experienced limited precipitation increases (BCI and BAI), and temperature increases (BCI), at sites closer to the treeline and with lower initial abundance of boreal species (BAI), and in Eurasia relative to Greenland-Iceland (BCI) and Western North America (BAI; **Figure 2**). Boreal species that contributed most towards borealization were those that had ranges extending into tundra species pools (i.e., boreal-tundra boundary species; **Figure 3**). Boreal species that colonised more frequently were shorter, and were more likely to be shrubs or graminoids than forbs (**Figure 4**).

Biogeography, climate and local conditions affected borealization

Our results indicate that borealization is strongly influenced by biogeoclimatic factors. Increased boreal abundance and colonisations were more likely to occur at high elevations (i.e., mountains) and boreal colonisations were more likely closer to treeline (**Figure 2b, g, i, k**), highlighting the role of boreal ecosystems as a current and future species source (Lloyd et al. 2002). Regionally, Eurasia experienced greater boreal increases than other regions, in line with modelling studies projecting a more pronounced movement of the taiga-tundra ecotone in Russia, among other regions (Tang et al. 2023). While the degree of borealization was highly variable across plant communities (**Figure 1, S3**), plots that became more 'borealized' (both via species colonisations and abundance increases) tended to be situated where climate had changed least (**Figure 2e, f, j**). Generally, these sites would be closer to the latitudinal treeline, although we did not find a correlation between warming and distance to treeline or latitude in our dataset, potentially due to the spatial heterogeneity of Arctic warming (IPCC 2021). More colonisations at warmer and wetter sites (**Figure 2c, d**) suggest that these conditions provide more favourable conditions for boreal-tundra plant establishment, as shown by experimental (Lynn et al. 2021) and observational studies (García Criado et al. 2020; Roland et al. 2021; Dial et al. 2022). Further, plots that experienced greater increases in boreal abundance had lower initial abundance of boreal plants (**Figure 2l**), indicating greater available niche space for boreal species to expand (Valladares et al. 2015). These findings suggest that borealization will occur not only close to boreal forests, but also where environmental and local conditions are more conducive to plant establishment.

Boreal colonisations were driven by boreal-tundra species and by shrubs and graminoids

We found that the boreal species contributing most to borealization were generally of short stature (**Figure 4a**) and more likely to be shrubs or graminoids than forbs (**Figure 4b**). This first result ran counter to our expectation that taller plants would be better colonisers, but could be explained by short species generally having lower seed mass (Thomas et al. 2020) and thus higher dispersal capacity. Additionally, shorter plants might be better able to cope with colder conditions, including frost and high wind speed (Bliss 1962), suggesting that relatively small boreal species might be able to succeed in harsher environments (Lynn et al. 2023). Conversely, in line with our hypothesis, shrubs and graminoids colonised 5.16 and 2.4 times more frequently than forbs, respectively (**Figure 4b**), possibly due to their inherent competitive advantages (Pajunen et al. 2011; Liu et al. 2018; Bråthen et al. 2021). Graminoids have deeper root networks and take up nutrients from the soil more readily, thus displacing shallow-rooted forb and shrub species. However, it should be noted that these traits were also associated with greater species losses, and thus reflect community turnover rates. In general, boreal colonisations seem to be driven by relatively more competitive species groups such as shrubs and graminoids, but also by shorter species that might be better adapted to Arctic environmental conditions.

While abundance change was similar across species classes (**Figure 3b**), boreal specialist species colonised plots 3 and 3.3 fewer times than boreal-tundra boundary and ubiquitous species (**Figure 3a**). This could indicate that species that are already present in local Arctic species pools (e.g., boreal-tundra boundary, ubiquitous) are better able to establish into new areas (e.g., through propagule pressure). Widespread species might be generalists and/or have broader bioclimatic envelopes, and could therefore increase in abundance and ultimately expand into new areas more efficiently than boreal specialist species (Timoney 2023), mirroring European trends with large-range species driving turnover (Staude et al. 2022). Species with populations that currently exist in the tundra likely have characteristics that allow them to survive in harsher environmental conditions, while boreal specialist species might not survive those environmental filters towards successful dispersal and establishment (Callaghan et al. 2004b). Thus, boreal specialist species might be limited in their abilities to colonise new tundra ecosystems.

The influx of boreal species could be intertwined with 'hidden diversity' as one of the main pathways of future community composition change. Hidden diversity refers to species present in local species pools that have not yet reached long-term monitoring plots (Pärtel 2014). With 64.4% of plot colonising species being present at the subsite level at the start of monitoring, many local colonisations were from species with a widespread distribution, which have the greatest potential to increase their abundance and distribution under climate change, rather than species migrating from the boreal forest (Callaghan et al. 2004b; Timoney 2023). Overall, our results indicate that borealization will likely be driven by widespread species with ranges extending into the Arctic that are present in local species pools, and not by boreal specialist species alone.

Considerations

Borealization is a process with multiple interacting variables. Here, we have attempted to remove correlations among variables by investigating the relationships between potential drivers (**Figure S2, S3**). There are certain considerations associated with field methods such as point-framing, where some extant species, particularly smaller ones, could be missed during surveys if not hit on exactly the same point and result in artificial colonisations and/or losses. However, this method has been generally considered to result in an accurate representation of plant communities (May and Hollister 2012). Acknowledging that 'top coloniser' species (**Table S3**) were also lost more frequently from plots because they are locally abundant within the landscape or they have high turnover rates (Staude et al. 2022), we focus here on colonisations and abundance increases to better understand the borealization process.

While in this study we focus on the process of borealization, negative borealization rates were observed at some sites (**Figure S4**), indicating a loss or reduced abundance of boreal species. Negative, slow or lagged rates of borealization may be due to stochastic processes and other factors that limit plant community change (Lenoir et al. 2020). For example, 1) herbivory can dampen species turnover (Speed et al. 2012), although herbivory was not a significant predictor of borealization in our analyses. This could be due to the coarse scale subsite-level herbivory information of the ITEX experimental design (Barrio et al. 2022). In addition, 2) some species including conifers (typically boreal species), have slow establishment rates, particularly at their northern range edges (Kroiss and HilleRisLambers 2015). 3) Plant recruitment and survival are highly sensitive to interannual climatic variation (Harsch et al. 2009), while climate-derived effects on reproduction can limit boreal treeline expansion (Brown et al. 2019). 4) Since our study sites are often far from the treeline, and not random in their distribution (Bjorkman et al. in prep), this could explain the low number of boreal specialist species within our dataset. Thus, more standardised studies at the boreal-tundra ecotone boundary are needed in order to refine estimates of the rate of spatial encroachment of boreal species. Future studies could characterise borealization at the landscape scale rather than plot scale, which might reveal somewhat different drivers.

Conclusions

Together, our findings suggest that future changes to tundra ecosystems might not involve rapid biome shifts where boreal species replace tundra species. Rather, we might expect an overall increase in the presence and abundance of species with broader geographic ranges that were already present within the Arctic, leading to a slower forest-tundra ecotone displacement into the tundra biome. Looking forward, we might expect borealization to not only occur at sites near the treeline, but also where boreal-tundra species are present in Arctic species pools. This borealization of tundra plant communities will have implications for wildlife habitats, trophic interactions and ecosystem functions. If tundra plant communities become more boreal, this could expand habitat for boreal herbivores such as beaver (*Castor canadensis*) and moose (Tape et al. 2018; Zhou et al. 2020), while simultaneously reducing habitat quality for tundra species such as barren-ground caribou (*Rangifer tarandus groenlandicus*; Fullman et al. 2017). Increased presence of boreal plant species within the tundra could also alter nutrient cycling and reduce soil carbon storage (Speed et al. 2015; Parker et al. 2021; Gustafson et al. 2021). Future research on the consequences of plant borealization will shed light on the implications for ecosystem functions and services over time, and ultimately the impacts for Arctic People.

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Plant community borealization in the Arctic is driven by boreal-tundra boundary species

Supplementary Information

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Supplementary Figures.

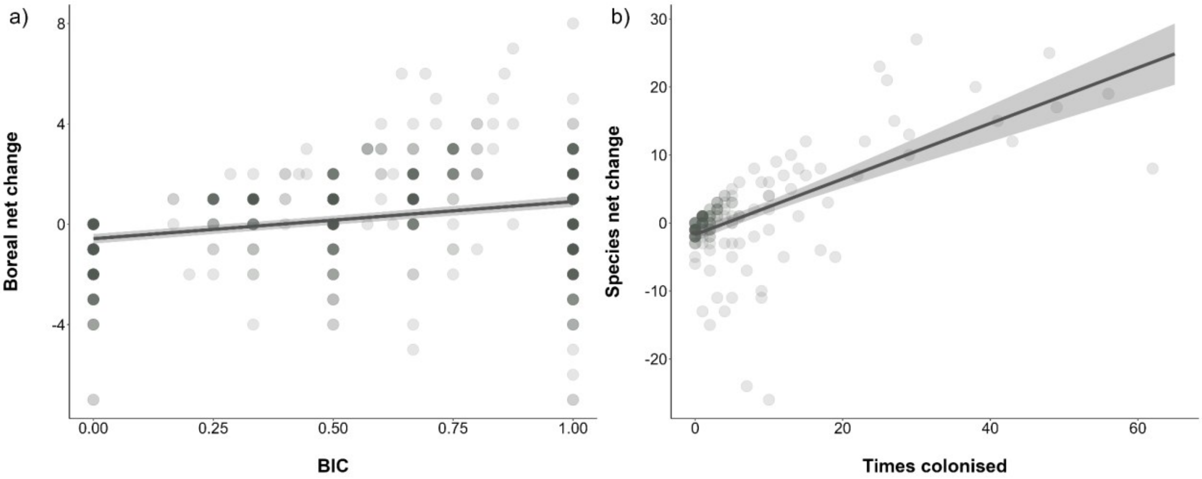
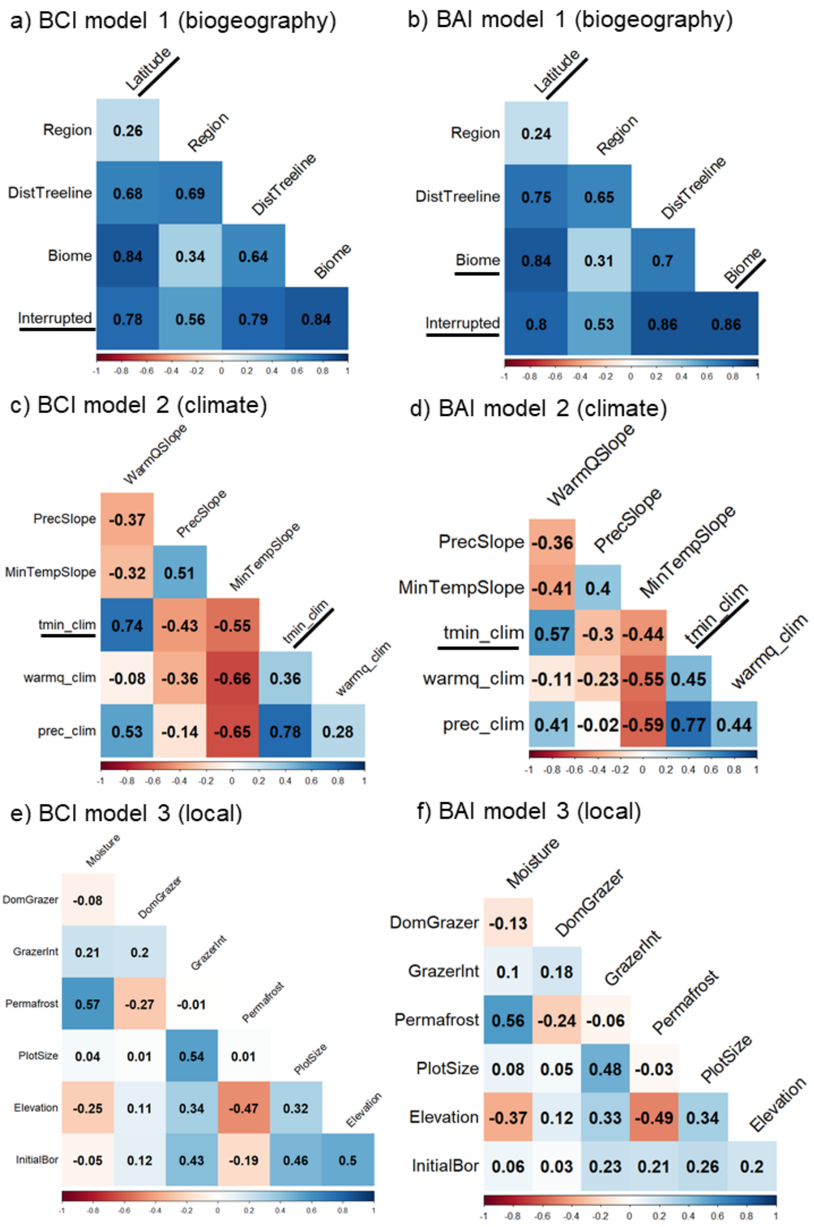


Figure S1. There were positive correlations between BCI and net change values at the community level (**a**) and between times colonised and net change at the species level (**b**). Darker grey colours indicate overlap of multiple points. Solid lines represent the model estimate, with credible intervals that did not overlap zero. Semi-transparent ribbons represent the 95% credible intervals.



a) BCI model 1 (biogeography)

b) BAI model 1 (biogeography)

c) BCI model 2 (climate)

d) BAI model 2 (climate)

e) BCI model 3 (local)

f) BAI model 3 (local)

Figure S2. Correlograms with the pairwise correlations for the fixed effects in each community-level model. Colour intensity is proportional to the correlation coefficients, with blue and red tones indicating positive and negative correlations, respectively. Underlined variables indicate those that were removed in community models due to high correlation (|Spearman's r| > 0.7) with other variables (see Methods). In order to include categorical variables in the pairwise correlations, we coded them as ordinal variables as follows: moisture (dry = 0, moist = 1, mixed = 2, wet = 3), dominant grazer (none = 0, insects = 1, small mammals = 2, birds = 3, mixed = 4, large mammals = 5), grazer intensity (low = 1, medium = 2, high = 3), permafrost (none = 0, sporadic = 1, continuous = 2), interruption to treeline (uninterrupted = 0, small water bodies = 1, mountains = 2, large water bodies = 3), biome (alpine = 0, Arctic = 1), biogeographic region (Eurasia = 1, Western North America = 2, Eastern North America = 3, Greenland-Iceland = 4).

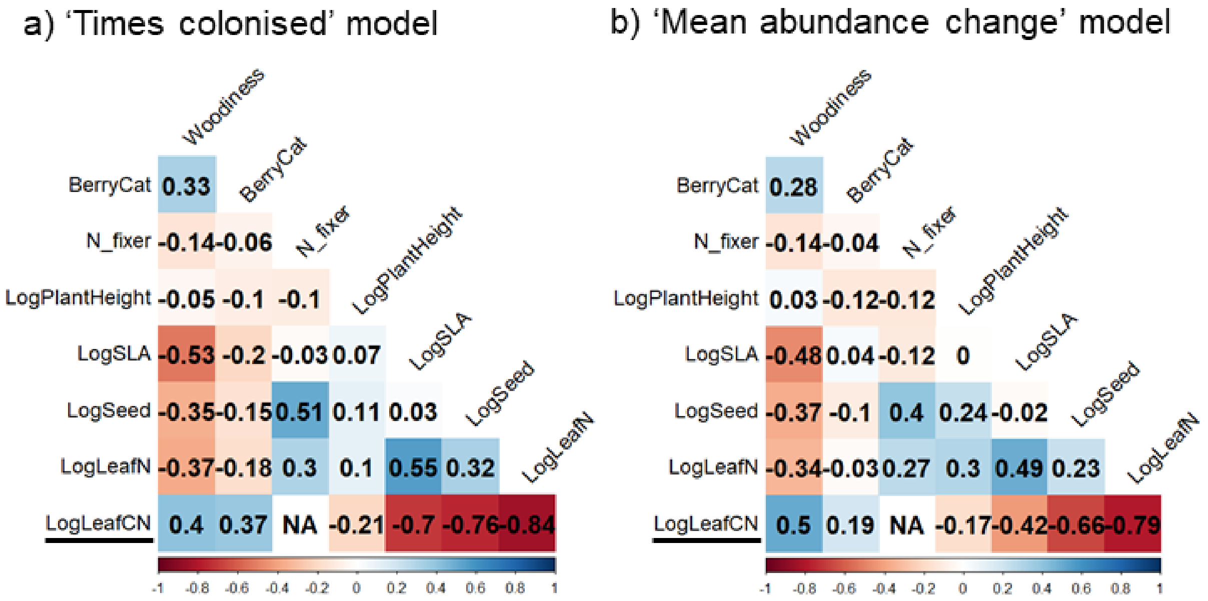
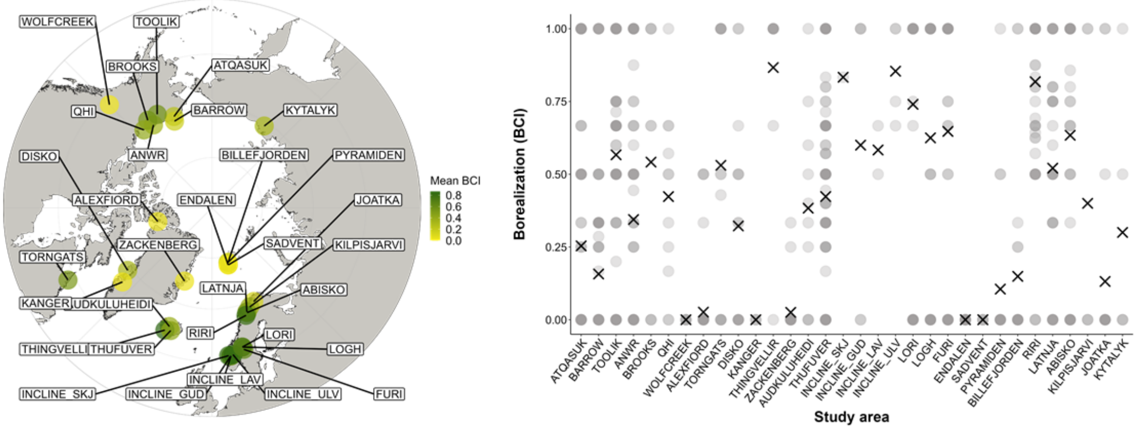


Figure S3. Correlogram with the pairwise correlations for the predictor variables in the species-level models. Colour intensity is proportional to the correlation coefficients, with blue and red tones indicating positive and negative correlations, respectively. The NA value between N_fixer and Leaf C:N is due to lack of variability in the data; all species with Leaf C:N data were non-fixers (i.e., 0 value). The underlined variable (leaf C:N) was removed in the species-level models due to high correlation with leaf N in both datasets, and with SLA and seed mass on the colonisation dataset (see Methods). Categorical traits were transformed to numerical variables for investigating correlations: berry production (not berry = 0, berry = 1), woodiness (not woody = 0, woody = 1), and N-fixer (0 = not fixer, 1 = fixer).

a) Study area full-range change (BCI)

b) Plot full-range change (BCI)



c) Study area full-range change (BAI)

d) Plot full-range change (BAI)

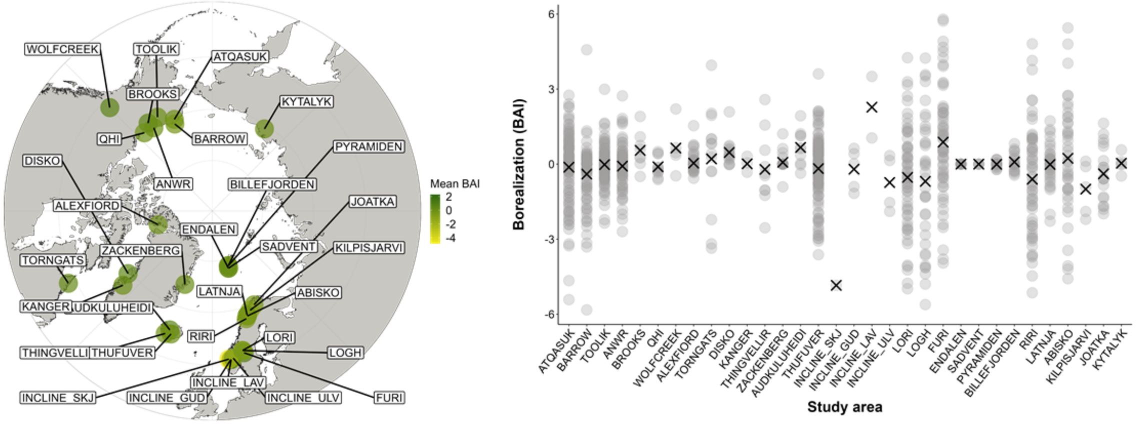
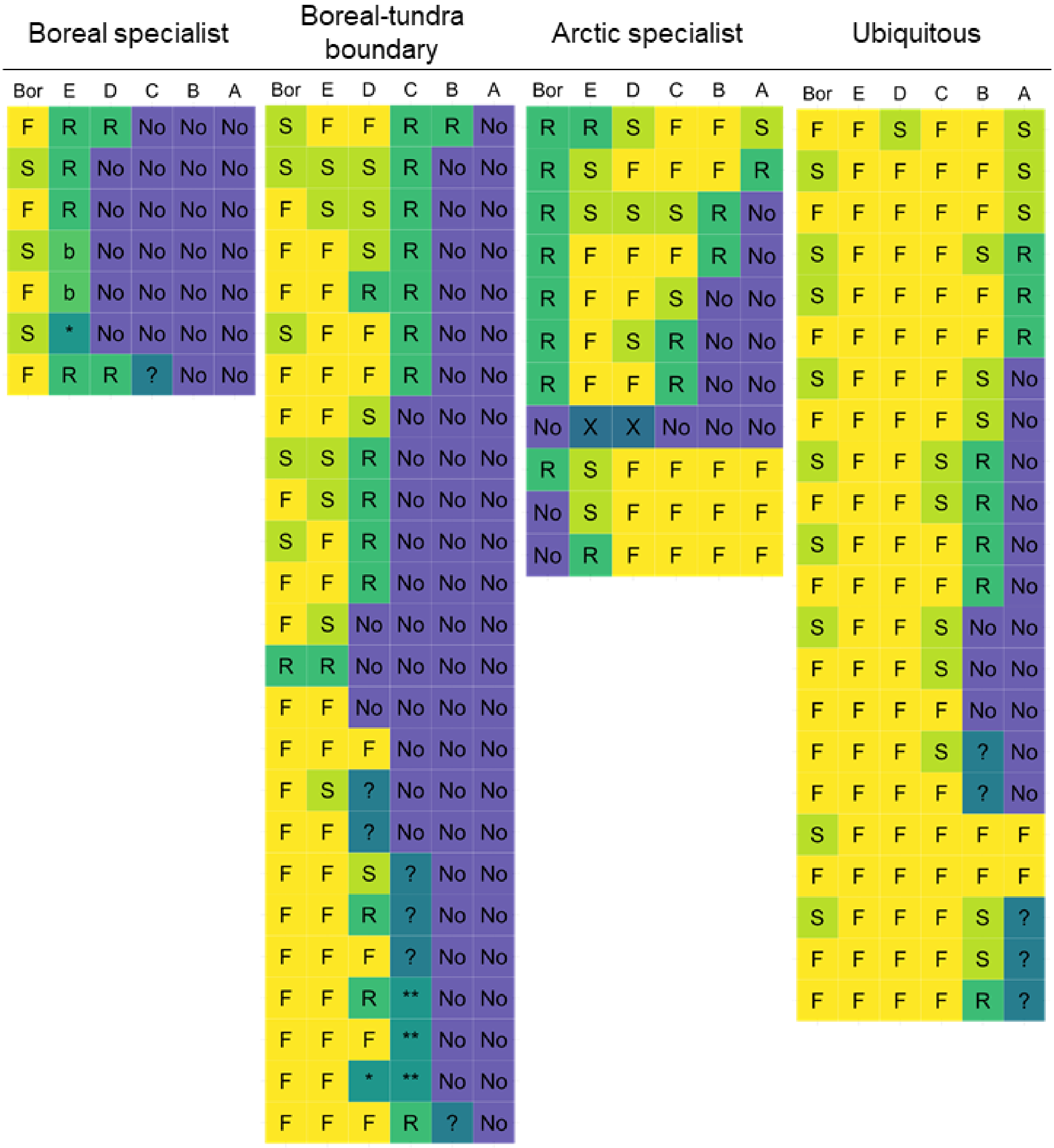


Figure S4. We detected wide variability in plant community borealization across the tundra when including plots that did not experience boreal colonisations (BCI = 0) and plots that experienced either no change or decreases in boreal species abundance (BAI <=0). The panel shows the distribution of the full range of change for boreal specialist and boreal-tundra boundary species across the tundra. **a)** Borealization estimated using colonisations as an average of all plots within a study area, **b)** BCI index for each plot within each study area, **c)** Borealization estimated using abundance change as an average of all plots within a study area, **d)** BAI index for each plot within each study area. Points in **a)** and **c)** are coloured according to the magnitude of increase (as BAI and BCI). Crosses indicate the mean value of the plot borealization index at the study area level in **b)** and **d)**, which represent the same value as coloured points in **a)** and **c)**. Study areas in **b)** and **d)** are arranged by longitude, and darker grey colours indicate overlap of multiple points.

Supplementary Tables

Table S1. Classification of species according to their presence and frequency in the different boreal and Arctic zones. We include in each column all the frequency combinations for the species in our dataset that we assigned to each class. Other possible frequency combinations for species not included in our dataset are not reflected here. The format in each row follows the following pattern: frequency in the Boreal zone (“Bor”), Zone E (“E”), Zone D (“D”), Zone C (“C”), Zone B (“B”) and Zone A (“A”), as indicated in the top row (Walker et al. 2005). Frequency in the different zones is specified and colour-coded as follows: No = not present, X = present without a frequency assessment, ? = uncertain, * = stabilized introductions, ** = casual introductions, R = rare, b = borderline Arctic species only present in the southernmost part of Zone E, S = scattered and F = frequent. The frequency in each zone is extracted from the Arctic Biodiversity Assessment (Meltofte 2013), and in particular from Appendix 9.1 (Daniëls et al. 2013), which lists all Arctic vascular plant species and their distribution in the five subzones based on Elven (2007). We considered a species to be present in a particular zone when it was reported as ‘scattered’ or ‘frequent’ in Daniëls et al. (2013); in contrast, we considered a species to be absent in a particular zone if it was described as ‘rare’, ‘uncertain’ or ‘introduced’.



Boreal specialist

Bor	E	D	C	B	A
F	R	R	No	No	No
S	R	No	No	No	No
F	R	No	No	No	No
S	b	No	No	No	No
F	b	No	No	No	No
S	*	No	No	No	No
F	R	R	?	No	No

Boreal-tundra boundary

Bor	E	D	C	B	A
S	F	F	R	R	No
S	S	S	R	No	No
F	S	S	R	No	No
F	F	S	R	No	No
F	F	R	R	No	No
S	F	F	R	No	No
F	F	F	R	No	No
F	F	S	No	No	No
S	S	R	No	No	No
F	S	R	No	No	No
S	F	R	No	No	No
F	F	R	No	No	No
F	S	No	No	No	No
R	R	No	No	No	No
F	F	No	No	No	No
F	F	F	No	No	No
F	S	?	No	No	No
F	F	?	No	No	No
F	F	S	?	No	No
F	F	R	?	No	No
F	F	F	?	No	No
F	F	R	**	No	No
F	F	F	**	No	No
F	F	*	**	No	No
F	F	F	R	?	No

Arctic specialist

Bor	E	D	C	B	A
R	R	S	F	F	S
R	S	F	F	F	R
R	S	S	S	R	No
R	F	F	F	R	No
R	F	F	S	No	No
R	F	S	R	No	No
R	F	F	R	No	No
No	X	X	No	No	No
R	S	F	F	F	F
No	S	F	F	F	F
No	R	F	F	F	F

Ubiquitous

Bor	E	D	C	B	A
F	F	S	F	F	S
S	F	F	F	F	S
F	F	F	F	F	S
S	F	F	F	S	R
S	F	F	F	F	R
F	F	F	F	F	R
S	F	F	F	S	No
F	F	F	F	S	No
S	F	F	S	R	No
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S	F	F	F	R	No
F	F	F	F	R	No
S	F	F	S	No	No
F	F	F	S	No	No
F	F	F	F	No	No
F	F	F	S	?	No
F	F	F	F	?	No
S	F	F	F	F	F
F	F	F	F	F	F
S	F	F	F	S	?
F	F	F	F	S	?
F	F	F	F	R	?

Table S2. Model structure for community- and species-level models. Borealization was quantified using BCI and BAI in community models, and as times colonised and mean cover change in the species-level models. Model structure is similar between ‘BCI’ and ‘BAI’ community models (*except for the BAI biogeographic model where biome was not included as a predictor), and between ‘times colonised’ and ‘mean cover change’ species models. Fixed effects are the retained variables after examining pairwise correlations among variables of interest. All community models included subsite as a random effect to account for spatial autocorrelation. Sample sizes are included in square brackets, first for the ‘positive-only’ models (i.e., including BCI and BAI values greater than zero) and then for ‘full-range’ models (i.e., including zeroes for BCI, and zeroes and negative values for BAI).

Community-level models (Borealization = BCI or BAI per plot)
Model 1: Biogeographic model [*n* = BCI: 598, 1,137; BAI: 488, 1137] Borealization ~ Biogeographic region + Distance to treeline + Biome* + (1|Subsite)
Model 2: Climatic model [*n* = BCI: 597, 1,130; BAI: 487, 1,130] Borealization ~ Warmest quarter temperature change + Precipitation change + Minimum Temperature change + Warmest quarter temperature climatology + Precipitation climatology + (1|Subsite)
Model 3: Local model [*n* = BCI: 581, 1,103; BAI: 466, 1,103] Borealization ~ Moisture + Grazing intensity + Dominant grazer + Elevation + Permafrost + Plot size + Initial boreal status + (1|Subsite)
Species-level models (Borealization = times colonised or mean cover per species) [*n* = 29 for times colonised model, *n* = 24 for abundance change model]
Borealization ~ Functional group + log(Plant height) + log(SLA) + log(Seed mass) + log(Leaf N)

Table S3. Summary of change and relevant traits per species, ordered by the number of times it colonised different plots. Plant species classes (Boreal specialist [B], Boreal-tundra boundary [BTB], Arctic specialist [A] and Ubiquitous [U]) are described in **Table S1**. 95% confidence intervals are calculated per species as (standard deviation/√n)*1.96. Species with NA values of mean plant height did not have enough records (minimum of 5) to be retained for species-level analysis. Sample size refers to the number of plots where the species were recorded in.

Order	Species	Functional group	Class	Times colonised	Mean cover change (% per year)	Cover change confidence intervals	Mean plant height (m)	Sample size
1	*Empetrum nigrum*	Shrub	U	72	0.27	0.16	0.10	469
2	*Persicaria vivipara*	Forb	U	67	0.08	0.12	0.09	345
3	*Carex bigelowii*	Graminoid	BTB	62	-0.08	0.07	0.09	536
4	*Betula nana*	Shrub	BTB	56	0.04	0.13	0.19	381
5	*Phyllodoce caerulea*	Shrub	BTB	49	0.11	0.18	0.07	123
6	*Vaccinium vitis-idaea*	Shrub	BTB	48	0.00	0.06	0.05	559
7	*Vaccinium myrtillus*	Shrub	BTB	43	0.02	0.17	0.09	219
8	*Silene acaulis*	Forb	U	42	-0.38	0.20	0.01	155
9	*Harrimanella hypnoides*	Shrub	BTB	41	-0.13	0.17	0.01	110
10	*Persicaria bistorta*	Forb	BTB	38	-0.03	0.06	NA	143
11	*Arctagrostis latifolia*	Graminoid	U	36	0.00	0.08	0.26	134

12	*Poa arctica*	Graminoid	U	36	0.39	0.21	0.14	137
13	*Stellaria longipes*	Forb	U	33	-0.10	0.11	0.06	112
14	*Salix arctica*	Shrub	U	31	0.23	0.16	0.04	236
15	*Pinguicula vulgaris*	Forb	BTB	30	0.09	0.04	0.08	37
16	*Pedicularis lapponica*	Forb	BTB	29	-0.05	0.08	0.07	61
17	*Thalictrum alpinum*	Forb	BTB	29	-0.07	0.12	0.06	78
18	*Cassiope tetragona*	Shrub	U	27	-0.17	0.10	0.09	291
19	*Rubus chamaemorus*	Forb	BTB	27	-0.03	0.09	0.06	117
20	*Petasites frigidus*	Forb	U	26	0.13	0.14	0.15	89
21	*Salix daphnoides*	Shrub	BTB	26	-0.26	0.15	0.35	163
22	*Salix lanata*	Shrub	BTB	25	0.28	0.20	1.48	32
23	*Eriophorum angustifolium*	Graminoid	U	24	0.38	0.21	0.25	143
24	*Vaccinium uliginosum*	Shrub	U	23	0.07	0.10	0.11	188
25	*Eriophorum vaginatum*	Graminoid	BTB	23	0.38	0.13	0.18	222
26	*Tofieldia pusilla*	Forb	BTB	22	0.00	0.08	0.11	56
27	*Deschampsia flexuosa*	Graminoid	BTB	19	-0.15	0.14	0.12	200

28	*Luzula confusa*	Graminoid	U	19	-0.22	0.09	0.12	149
29	*Luzula nivalis*	Graminoid	A	19	-0.17	0.14	0.10	96
30	*Pyrola grandiflora*	Forb	U	19	-0.02	0.07	0.05	49
31	*Kobresia myosuroides*	Graminoid	U	19	0.11	0.17	NA	60
32	*Saxifraga cernua*	Forb	U	18	-0.08	0.16	0.10	60
33	*Saxifraga hirculus*	Forb	U	18	-0.01	0.15	0.18	52
34	*Calluna vulgaris*	Shrub	BTB	18	0.42	0.41	0.17	105
35	*Micranthes punctata*	Forb	BTB	17	0.00	0.09	NA	44
36	*Tephroseris integrifolia*	Forb	BTB	17	-0.03	0.06	0.15	51
37	*Dupontia fisheri*	Graminoid	U	17	-0.27	0.39	0.17	83
38	*Saxifraga oppositifolia*	Forb	U	16	-0.14	0.29	NA	65
39	*Trisetum spicatum*	Graminoid	U	16	0.29	0.19	0.24	46
40	*Luzula spicata*	Graminoid	BTB	15	0.06	0.07	0.13	25
41	*Carex microcarpa*	Graminoid	U	15	0.43	0.26	0.22	145
42	*Rhododendron tomentosum*	Shrub	BTB	15	-0.21	0.10	0.08	235
43	*Salix polaris*	Shrub	A	15	-0.05	0.32	0.04	117

44	*Solidago virgaurea*	Forb	BTB	14	0.15	0.12	0.12	74
45	*Oxyria digyna*	Forb	U	14	-0.10	0.08	0.17	80
46	*Salix herbacea*	Shrub	U	14	-0.14	0.17	0.02	214
47	*Ranunculus nivalis*	Forb	U	14	-0.09	0.11	0.10	27
48	*Minuartia stricta*	Forb	BTB	14	0.17	0.10	NA	26
49	*Bartsia alpina*	Forb	BTB	13	0.11	0.08	0.08	21
50	*Andromeda polifolia*	Shrub	BTB	13	0.01	0.17	0.05	60
51	*Pedicularis hirsuta*	Forb	U	13	0.03	0.10	0.08	21
52	*Hierochloe pauciflora*	Graminoid	U	13	0.43	0.42	0.13	27
53	*Salix glauca*	Shrub	BTB	12	0.22	0.20	0.46	47
54	*Oreojuncus trifidus*	Graminoid	BTB	12	0.01	0.06	0.09	43
55	*Festuca richardsonii*	Graminoid	U	12	0.00	0.29	0.31	80
56	*Arctous alpina*	Shrub	U	11	-0.02	0.16	0.05	43
57	*Saussurea alpina*	Forb	BTB	11	0.39	0.42	0.17	13
58	*Pedicularis capitata*	Forb	U	11	-0.03	0.07	0.08	31
59	*Hierochloe alpina*	Graminoid	U	11	0.12	0.14	0.24	50

60	*Astragalus alpinus*	Forb	BTB	10	0.23	0.26	0.08	25
61	*Juniperus communis*	Shrub	BTB	10	-0.77	0.85	0.60	23
62	*Juncus biglumis*	Graminoid	U	10	0.10	0.11	0.08	20
63	*Salix rotundifolia*	Shrub	BTB	10	-0.63	0.28	0.02	53
64	*Saussurea angustifolia*	Forb	BTB	10	0.01	0.06	0.13	24
65	*Armeria maritima*	Forb	BTB	10	-0.36	0.10	0.19	100
66	*Sagina nivalis*	Forb	A	10	0.31	0.05	0.02	10
67	*Viola biflora*	Forb	BTB	10	0.18	0.15	0.04	32
68	*Salix reticulata*	Shrub	U	9	0.32	0.16	0.05	111
69	*Lysimachia europaea*	Forb	BTB	9	-0.03	0.03	0.04	77
70	*Diapensia lapponica*	Shrub	U	9	-0.03	0.12	0.03	40
71	*Sibbaldia procumbens*	Forb	BTB	9	-0.01	0.16	0.03	24
72	*Agrostis mertensii*	Graminoid	BTB	9	-0.29	0.17	0.14	39
73	*Pedicularis flammea*	Forb	A	9	0.05	0.10	NA	16
74	*Carex rupestris*	Graminoid	U	8	-0.06	0.14	NA	30
75	*Calamagrostis lapponica*	Graminoid	BTB	8	-0.08	0.19	0.19	91

76	*Deschampsia cespitosa*	Graminoid	BTB	8	-0.08	0.29	0.60	22
77	*Dryas integrifolia*	Shrub	U	8	-0.12	0.10	0.06	125
78	*Pedicularis lanata*	Forb	U	8	0.03	0.14	0.08	28
79	*Anthoxanthum odoratum*	Graminoid	B	8	-0.43	0.57	0.26	19
80	*Festuca ovina*	Graminoid	BTB	7	0.05	0.30	0.35	36
81	*Carex fuliginosa*	Graminoid	U	7	-0.06	0.09	NA	24
82	*Festuca rubra*	Graminoid	U	7	0.11	0.36	0.31	25
83	*Potentilla hyparctica*	Forb	U	7	-0.10	0.09	0.07	26
84	*Micranthes foliolosa*	Forb	U	7	-0.26	0.22	0.09	22
85	*Luzula multiflora*	Graminoid	BTB	7	0.01	0.03	0.15	45
86	*Rhodiola rosea*	Forb	U	7	0.08	0.20	0.11	15
87	*Eriophorum scheuchzeri*	Graminoid	U	6	0.21	0.14	0.24	6
88	*Salix phlebophylla*	Shrub	BTB	6	0.06	0.26	0.02	54
89	*Alopecurus alpinus*	Graminoid	U	6	-0.11	0.44	0.21	24
90	*Cochlearia officinalis*	Forb	BTB	6	-0.03	0.13	0.15	14
91	*Poa pratensis*	Graminoid	U	6	-0.16	0.10	0.28	29

92	*Luzula arcuata*	Graminoid	BTB	6	-0.02	0.09	NA	11
93	*Galium boreale*	Forb	BTB	6	0.75	0.42	0.28	6
94	*Dryas octopetala*	Shrub	U	5	0.03	0.28	0.05	89
95	*Rhododendron lapponicum*	Shrub	U	5	-0.01	0.33	0.08	29
96	*Cardamine bellidifolia*	Forb	U	5	0.20	0.18	NA	6
97	*Oreomecon radicata*	Forb	B	5	-0.08	0.08	0.11	22
98	*Cerastium alpinum*	Forb	U	5	-0.04	0.08	NA	15
99	*Oxytropis nigrescens*	Forb	U	5	0.04	0.13	NA	19
100	*Pedicularis sudetica*	Forb	U	5	-0.14	0.21	0.08	13
101	*Carex rotundata*	Graminoid	BTB	5	0.08	0.82	NA	10
102	*Carex capillaris*	Graminoid	BTB	5	-0.05	0.12	NA	12
103	*Cardamine pratensis*	Forb	U	5	-0.30	0.17	0.18	25
104	*Cerastium arcticum*	Forb	A	5	0.03	0.14	0.11	20
105	*Carex microglochin*	Graminoid	BTB	5	0.14	0.10	NA	5
106	*Ranunculus acris*	Forb	BTB	5	0.11	0.12	0.24	14
107	*Kalmia procumbens*	Shrub	BTB	5	0.42	0.62	0.04	13

108	*Cardamine digitalis*	Forb	BTB	5	0.05	0.05	0.05	6
109	*Gnaphalium supinum*	Forb	BTB	5	-0.04	0.29	0.05	18
110	*Vahlodea atropurpurea*	Graminoid	BTB	5	0.02	0.04	NA	11
111	*Euphrasia frigida*	Forb	A	5	-0.05	0.08	0.08	12
112	*Minuartia biflora*	Forb	U	5	0.07	0.02	NA	5
113	*Calamagrostis inexpansa*	Graminoid	B	5	-0.09	0.15	NA	25
114	*Poa glauca*	Graminoid	U	4	-0.27	0.42	0.26	8
115	*Calamagrostis stricta*	Graminoid	U	4	0.29	0.42	0.15	13
116	*Oxytropis maydelliana*	Forb	U	4	-0.09	0.14	0.09	16
117	*Oxytropis campestris*	Forb	BTB	4	0.08	0.24	0.11	9
118	*Carex rariflora*	Graminoid	BTB	4	0.45	0.84	0.28	13
119	*Festuca vivipara*	Graminoid	BTB	4	0.17	0.30	0.14	8
120	*Cerastium beeringianum*	Forb	U	4	-0.46	0.37	NA	19
121	*Festuca altaica*	Graminoid	BTB	4	0.39	0.15	NA	7
122	*Alopecurus magellanicus*	Graminoid	U	4	0.50	0.86	0.13	12
123	*Betula pubescens*	Shrub	BTB	4	0.11	0.11	2.34	5

124	*Hieracium alpinum*	Forb	BTB	4	-0.04	0.04	0.13	76
125	*Galium verum*	Forb	BTB	4	0.83	0.78	0.15	5
126	*Salix hastata*	Shrub	BTB	3	0.28	0.40	NA	9
127	*Salix chamissonis*	Shrub	BTB	3	-0.06	0.26	NA	11
128	*Linnaea borealis*	Shrub	BTB	3	0.02	0.50	0.05	6
129	*Festuca brachyphylla*	Graminoid	U	3	-0.20	0.29	0.12	11
130	*Arnica griscomii*	Forb	BTB	3	0.19	0.54	NA	4
131	*Hedysarum alpinum*	Forb	BTB	3	0.07	0.10	NA	12
132	*Antennaria friesiana*	Forb	U	3	0.11	0.25	0.10	4
133	*Draba lactea*	Forb	U	3	0.02	0.23	0.05	11
134	*Calamagrostis holmii*	Graminoid	BTB	3	0.27	0.03	0.13	3
135	*Micranthes hieraciifolia*	Forb	U	3	0.03	0.12	NA	16
136	*Stellaria crassipes*	Forb	U	3	0.23	0.23	0.06	4
137	*Veronica alpina*	Forb	U	3	-0.01	0.09	0.07	15
138	*Pyrola minor*	Forb	BTB	3	0.24	0.36	0.10	9
139	*Rumex acetosa*	Forb	BTB	3	-0.04	0.07	0.32	18

140	*Gentiana nivalis*	Forb	BTB	3	0.08	0.14	0.08	4
141	*Antennaria alpina*	Forb	BTB	3	0.05	0.22	0.11	5
142	*Festuca baffinensis*	Graminoid	U	3	-0.09	0.23	0.15	6
143	*Euphrasia arctica*	Forb	B	3	0.37	0.25	NA	4
144	*Chamorchis alpina*	Forb	B	2	-0.03	0.26	NA	3
145	*Gymnadenia conopsea*	Forb	BTB	2	0.17	0.07	0.40	2
146	*Pinguicula villosa*	Forb	BTB	2	0.03	0.03	NA	5
147	*Orthilia secunda*	Forb	BTB	2	-0.05	0.05	0.11	12
148	*Braya purpurascens*	Forb	U	2	-0.04	0.14	NA	6
149	*Salix planifolia*	Shrub	BTB	2	0.01	0.30	0.44	44
150	*Astragalus umbellatus*	Forb	BTB	2	-0.47	0.28	0.09	21
151	*Carex x turfosa*	Graminoid	BTB	2	-0.05	0.06	0.19	6
152	*Anemone parviflora*	Forb	BTB	2	0.10	0.22	NA	8
153	*Arctous rubra*	Shrub	BTB	2	-0.01	0.20	NA	13
154	*Lupinus arcticus*	Forb	BTB	2	0.54	0.41	0.17	16
155	*Pedicularis verticillata*	Forb	BTB	2	-0.02	0.09	0.14	7

156	*Salix fuscescens*	Shrub	BTB	2	0.15	0.99	NA	6
157	*Valeriana capitata*	Forb	BTB	2	-0.06	0.10	0.19	6
158	*Ranunculus pallasii*	Forb	BTB	2	0.07	0.35	NA	3
159	*Poa alpina*	Graminoid	U	2	-0.14	0.11	0.19	19
160	*Silene uralensis*	Forb	U	2	0.15	0.05	0.04	2
161	*Carex fimbriata*	Graminoid	B	2	-0.16	0.21	0.22	9
162	*Pedicularis dasyantha*	Forb	A	2	0.10	0.21	NA	6
163	*Silene apetala*	Forb	U	2	0.16	0.37	NA	4
164	*Phleum alpinum*	Graminoid	BTB	2	-0.07	0.09	0.27	12
165	*Pyrola rotundifolia*	Forb	BTB	2	0.32	0.37	0.23	3
166	*Carex lachenalii*	Graminoid	U	2	-0.40	0.16	0.11	46
167	*Carex brunnescens*	Graminoid	BTB	2	-0.60	0.32	0.11	23
168	*Salix phylicifolia*	Shrub	BTB	2	0.20	0.08	2.69	2
169	*Carex parallela*	Graminoid	U	1	-0.59	0.52	NA	19
170	*Carex vaginata*	Graminoid	BTB	1	-0.43	0.24	0.09	45
171	*Astragalus frigidus*	Forb	BTB	1	-0.16	0.21	NA	4

172	*Vaccinium microcarpum*	Shrub	BTB	1	0.32	0.31	NA	6
173	*Carex ericetorum*	Graminoid	B	1	0.36	0.24	0.22	15
174	*Kobresia simpliciuscula*	Graminoid	U	1	0.18	NA	NA	1
175	*Silene involucrata*	Forb	U	1	0.07	NA	NA	1
176	*Androsace ochotensis*	Forb	A	1	0.50	NA	NA	1
177	*Eutrema edwardsii*	Forb	U	1	-0.20	0.18	NA	8
178	*Oxytropis borealis*	Forb	BTB	1	-0.11	0.16	NA	11
179	*Salix niphoclada*	Shrub	BTB	1	0.04	0.22	0.44	5
180	*Hedysarum boreale*	Forb	BTB	1	0.05	0.15	NA	2
181	*Pedicularis labradorica*	Forb	BTB	1	0.09	0.26	NA	2
182	*Minuartia arctica*	Forb	U	1	-0.12	0.42	NA	2
183	*Carex chordorrhiza*	Graminoid	BTB	1	0.26	NA	NA	1
184	*Luzula wahlenbergii*	Graminoid	U	1	-0.04	0.20	0.20	2
185	*Papaver lapponicum*	Forb	U	1	-0.15	0.18	0.13	5
186	*Carex subspathacea*	Graminoid	U	1	-1.13	1.35	0.09	7
187	*Arctophila fulva*	Graminoid	U	1	-0.07	0.39	NA	3

188	*Ranunculus pygmaeus*	Forb	U	1	-0.63	1.78	0.05	2
189	*Cerastium regelii*	Forb	A	1	0.71	NA	NA	1
190	*Carex mackenziei*	Graminoid	BTB	1	-0.09	0.23	NA	2
191	*Saxifraga tricuspidata*	Forb	U	1	-0.11	0.26	NA	2
192	*Draba nivalis*	Forb	U	1	-0.58	0.48	NA	6
193	*Aconitum septentrionale*	Forb	BTB	1	0.54	NA	1.00	1
194	*Agrostis capillaris*	Graminoid	BTB	1	-0.02	1.34	0.39	10
195	*Euphrasia wettsteinii*	Forb	U	1	0.06	0.13	NA	7
196	*Potentilla erecta*	Forb	B	1	0.28	0.61	0.20	4
197	*Scorzoneroides autumnalis*	Forb	BTB	1	0.16	0.23	0.16	9
198	*Viola palustris*	Forb	BTB	1	0.29	0.63	0.12	7
199	*Dactylorhiza viridis*	Forb	BTB	1	0.00	0.31	0.22	2
200	*Parnassia palustris*	Forb	BTB	1	0.03	0.09	0.13	3
201	*Potentilla crantzii*	Forb	U	1	-0.07	0.23	0.13	9
202	*Cerastium cerastoides*	Forb	BTB	1	0.05	0.20	0.04	5
203	*Trollius europaeus*	Forb	BTB	1	0.03	0.21	0.50	2

204	*Taraxacum croceum*	Forb	BTB	1	0.01	0.10	NA	2
205	*Rumex alpestris*	Forb	BTB	1	0.07	NA	0.32	1
206	*Micranthes nelsoniana*	Forb	U	1	-0.02	0.10	0.15	2
207	*Lagotis minor*	Forb	U	1	0.02	NA	0.14	1
208	*Galium normanii*	Forb	B	1	0.35	NA	NA	1
209	*Avenella flexuosa*	Graminoid	BTB	1	-0.17	0.99	NA	4
210	*Koenigia islandica*	Forb	U	1	0.43	NA	0.04	1
211	*Thymus praecox*	Shrub	BTB	1	0.09	NA	0.09	1
212	*Arnica lessingii*	Forb	BTB	1	0.12	NA	NA	1
213	*Lagotis glauca*	Forb	U	1	-0.05	0.19	0.14	3
214	*Polemonium acutiflorum*	Forb	BTB	1	0.08	NA	0.40	1
215	*Geum glaciale*	Forb	U	1	0.09	NA	NA	1
216	*Ranunculus lapponicus*	Forb	U	1	-0.16	0.87	NA	2
217	*Epilobium latifolium*	Forb	U	1	0.16	0.23	0.16	2
218	*Salix uva-ursi*	Shrub	BTB	1	-0.25	0.91	NA	3
219	*Salix arctophila*	Shrub	BTB	1	0.87	1.49	0.09	2

220	*Carex supina*	Graminoid	BTB	1	0.34	0.88	NA	4
221	*Pseudorchis albida*	Forb	B	0	-0.14	NA	0.22	1
222	*Carex atrata*	Graminoid	BTB	0	-0.08	0.06	0.22	7
223	*Carex marina*	Graminoid	A	0	-0.27	0.16	NA	7
224	*Carex microchaeta*	Graminoid	BTB	0	-0.20	0.32	NA	8
225	*Artemisia norvegica*	Forb	B	0	0.05	0.16	NA	6
226	*Boykinia richardsonii*	Forb	BTB	0	0.77	NA	NA	1
227	*Salix alaxensis*	Shrub	BTB	0	-0.30	0.33	1.65	8
228	*Astragalus eucosmus*	Forb	BTB	0	-0.04	0.02	NA	2
229	*Cardamine digitata*	Forb	BTB	0	-0.36	0.52	0.05	3
230	*Doronicum grandiflorum*	Forb	B	0	-0.09	0.05	NA	2
231	*Senecio lugens*	Forb	BTB	0	-0.03	NA	NA	1
232	*Eriophorum chamissonis*	Graminoid	BTB	0	-0.09	0.14	0.18	3
233	*Oxytropis deflexa*	Forb	BTB	0	-0.16	NA	NA	1
234	*Carex scirpoidea*	Graminoid	BTB	0	0.02	NA	0.12	1
235	*Kobresia sibirica*	Graminoid	A	0	-0.08	NA	NA	1

236	*Minuartia obtusiloba*	Forb	BTB	0	-0.05	0.30	NA	2
237	*Draba micropetala*	Forb	A	0	-0.13	0.11	0.04	2
238	*Stellaria humifusa*	Forb	U	0	-0.28	0.08	NA	5
239	*Chrysosplenium tetrandrum*	Forb	U	0	-0.31	0.13	0.02	2
240	*Gentianella propinqua*	Forb	BTB	0	-0.20	0.03	0.10	2
241	*Potentilla fruticosa*	Shrub	BTB	0	-0.05	0.08	0.48	2
242	*Salix arbusculoides*	Shrub	BTB	0	-0.10	NA	0.27	1
243	*Saxifraga flagellaris*	Forb	A	0	-0.09	NA	NA	1
244	*Luzula parviflora*	Graminoid	BTB	0	-0.04	NA	NA	1
245	*Saxifraga cespitosa*	Forb	U	0	-0.47	0.25	NA	2
246	*Achillea millefolium*	Forb	BTB	0	0.32	0.41	0.15	3
247	*Alchemilla alpina*	Forb	BTB	0	0.00	0.66	0.11	9
248	*Campanula rotundifolia*	Forb	BTB	0	-0.08	0.15	0.25	6
249	*Carex flava*	Graminoid	B	0	-0.16	0.04	0.49	2
250	*Cerastium fontanum*	Forb	BTB	0	-0.20	0.29	0.25	4
251	*Geranium sylvaticum*	Forb	BTB	0	0.22	0.68	0.41	3

252	*Nardus stricta*	Graminoid	BTB	0	-1.48	2.05	0.21	6
253	*Rhinanthus minor*	Forb	BTB	0	0.04	0.29	0.35	3
254	*Sagina saginoides*	Forb	BTB	0	-0.20	0.03	0.07	2
255	*Omalotheca supina*	Forb	BTB	0	-0.54	0.68	NA	4
256	*Pilosella officinarum*	Forb	B	0	-0.35	1.61	0.08	2
257	*Epilobium anagallidifolium*	Forb	BTB	0	-0.14	0.17	0.07	2
258	*Antennaria pulchella*	Forb	A	0	0.18	NA	NA	1
259	*Saxifraga aizoides*	Forb	U	0	-0.06	NA	0.08	1
260	*Lycopodium complanatum*	Forb	B	0	-0.01	0.00	0.09	2
261	*Erigeron humilis*	Forb	U	0	-0.31	0.28	NA	9
262	*Antennaria dioica*	Forb	BTB	0	-0.03	NA	0.10	1
263	*Agrostis vinealis*	Graminoid	BTB	0	-1.39	0.00	0.49	2
264	*Micranthes nivalis*	Forb	U	0	-0.16	NA	0.09	1
265	*Arabidopsis lyrata*	Forb	U	0	-0.06	NA	NA	1
266	*Androsace chamaejasme*	Forb	BTB	0	-0.27	NA	NA	1
267	*Betula glandulosa*	Shrub	BTB	0	0.16	1.67	0.56	5

268	*Veronica wormskjoldii*	Forb	BTB	0	-0.18	NA	NA	1
269	*Potentilla uniflora*	Forb	BTB	0	-0.12	NA	NA	1
270	*Carex nardina*	Graminoid	U	0	0.23	4.01	NA	2
271	*Arenaria pseudofrigida*	Forb	U	0	-0.91	NA	NA	1
272	*Lesquerella arctica*	Forb	U	0	-0.45	NA	NA	1

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