Borealization of plant communities in the Arctic is driven by boreal-tundra species

Running title: Tundra plant borealization

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Abstract

Following rapid climate change, tundra plant communities are experiencing extensive compositional shifts. A conservation concern is the potential encroachment of boreal species into the tundra (‘borealization’). Tundra borealization has been sporadically reported, but not systematically quantified. Here, we synthesized data from across 32 study areas, spanning 1,137 plots and 287 vascular plant species, resurveyed between 1981 and 2023. We i) quantified tundra borealization as the colonisation and increase in abundance of Boreal and Boreal-Tundra species, ii) assessed biogeographical, climatic and local borealization drivers, and iii) identified species contributing to borealization and their associated traits. Half of the plots experienced borealization, although borealization rates were not different to random expectation. Borealization was greater in Eurasia, closer to the treeline, at higher elevations, in warmer and wetter regions, where climate change was limited, and where initial boreal abundance was lower. Boreal coloniser species were generally short-statured, and more often shrubs and graminoids. Boreal species colonised around three times less frequently than Boreal-Tundra species. Hence, our findings indicate that tundra borealization is mainly driven by the spread of already established boreal-low Arctic tundra species. These plant community composition changes could have cascading impacts on land-atmosphere interactions, trophic dynamics and local and Indigenous livelihoods.

Introduction

Climate change is leading to widespread vegetation change in tundra regions (Elmendorf *et al.* 2012; García Criado *et al.* 2025; Myers-Smith *et al.* 2011). 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 (Frost & Epstein 2014; Harsch *et al.* 2009; 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 (Emblemsvåg *et al.* 2022; Pecuchet *et al.* 2020), terrestrial studies are lagging far behind (Verdonen et al. 2025). Within the tundra, range expansions of boreal animals such as red fox (*Vulpes vulpes*), moose (*Alces alces*) and songbirds have been reported (Elmhagen *et al.* 2017; Le Pogam *et al.* 2021; Tape *et al.* 2016), and recent modelling shows northward movement of boreal herbivores following 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 & Boudreau 2012), especially those with no dispersal barriers (Rupp *et al.* 2001). Similarly, warmer conditions could favour boreal species as they inhabit a warmer thermal niche than tundra species (Lynn *et al.* 2021; Villén-Peréz *et al.* 2020). This could result in regional differences in borealization, since for example Arctic Europe (Palaearctic) is generally warmer than Arctic North America (Nearctic; Callaghan *et al.* 2004b). 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 intermediate and local 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 (Lynn *et al.* 2021; Vincent *et al.* 2020) and are more likely to expand across tundra habitats (Callaghan *et al.* 2004a). 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 (García Criado *et al.* 2023; Vuorinen *et al.* 2017). 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 (Kaarlejärvi *et al.* 2017; Pajunen *et al.* 2011; 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 in tundra ecosystems due to vegetation change, which together with enhanced permafrost thaw, could 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 & Boyce 2018) and local and Indigenous communities (Hupp *et al.* 2015; Rees *et al.* 2008).

Here, we synthesized observations of plant composition from across the Arctic to address the following research questions (RQs):

> RQ1. How much borealization has occurred across the tundra biome over the past four decades?
>
> We expect that the majority of sites will have experienced an increase in boreal species presence and abundance, based on evidence from a few 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.* 2004b).
>
> 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.* 2004a; 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 (Behrend *et al.* 2024; Myers-Smith *et al.* 2011). 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 synthesized observations of plant composition from the database of the International Tundra Experiment (ITEX+; Bjorkman et al. in prep., Henry and Molau 1997), a geographically distributed experiment with a pan-Arctic extent and standardised study design and data collection (Molau & Mølgaard 1996). 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 in the Northern Hemisphere 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, which were then categorised as Arctic (n = 642 plots within 71 subsites and 15 sites) and alpine (n = 495 plots within 42 subsites and 17 sites) categories for analysis. 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). Plots were our replication unit for analyses, with an average size of 3.86 m^2 (range = 0.05 - 120).

We followed the protocol published in García Criado et al. (2025) 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). Thus, total cover in each plot-by-year always added up to 100%. We retained only vascular plants since non-vascular plants are not recorded consistently across the ITEX+ dataset, and removed abiotic records (e.g., rocks, soil, etc.) prior to cover calculations. In total, 37,031 abiotic and non-vascular records were removed. 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. Since the presence of ecotypes and an evolving taxonomy is a well-known issue for tundra plants, we assigned the latest accepted synonym from WorldFlora Online for consistency among species.

Species classification

While there are different methods to categorise species according to their native distributions, 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 abundant 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 across the boreal and tundra biomes (Elven 2007; Walker *et al.* 2005):

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

These classes are relative to these two biomes and are not intended to reflect the full range of species distributions in other biomes (e.g., a ‘Boreal’ species could also extend into the temperate forest). While the number of species included in each class is relatively unbalanced, the species classification reflects the ecological nature of the species and the distribution of the ITEX network within the tundra biome. Hereafter, we consider ‘boreal’ (in lowercase) to include species distributed across the biome boundary but not extending into the High Arctic (i.e., Boreal and Boreal-Tundra species classes). Note that Boreal is capitalized when referring to the specific species class, and the term ‘boreal’ encompasses both Boreal and Boreal-Tundra classes. We consider Boreal-Tundra 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 (Aarnes *et al.* 2012; Birks 2008), underscoring the importance of warmer periods following deglaciation. Thus, expansions of these species represent long-term borealization processes. Boreal-Tundra 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, using two complementary indices to better untangle these two processes of plant community change. 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 influx of new boreal species into a plot over time. BCI reflects the proportion of colonisers that are boreal species (Boreal and Boreal-Tundra species), and is bound between 0 and 1. Thus, a value of BCI = 1 does not mean that the plot is composed exclusively of boreal species, rather, that all the plot colonisations are from boreal species. Duration is not explicitly included in this formula because we were interested in the proportion of total colonisations that were boreal. Still, 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 boreal cover (Boreal and Boreal-Tundra 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. Because total cover in each plot-by-year always added up to 100%, any increase in boreal species abundance can be interpreted as a parallel decline of Arctic and Ubiquitous species, and vice versa. 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.

In order to understand whether BCI and BAI reflected actual borealization dynamics or background community turnover, we contrasted our observed index values with a null model. The BCI null model was built by resampling 999 times the species classes for all the species present in each study area over the study period, and subsequently calculating mean BCI per plot from this randomization, together with the interval encompassing ± 2 SD. For BAI, we similarly randomized 999 times the species classes and we calculated cover change as the difference between end and start cover for the simulated boreal species. To assess similarity between observed and simulated values, we compared the observed values to the simulated mean BCI and BAI ± 2 SD per plot.

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 of summer temperatures, minimum annual temperature and annual precipitation, and their associated 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 categorised barriers to dispersal 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 & 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 this outlier, CHELSA remains the most appropriate choice for our climate data due to its very fine resolution at 1x1 km and because its quasi-mechanistical statistical downscaling has outperformed other interpolation-based climatic data sources, particularly for precipitation (Karger *et al.* 2017).

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). Herbivory intensity was categorised as low, medium and high. Dominant grazer included: none, insects, birds, small mammals and large mammals. Moisture was also a categorical variable: dry, moist, wet and mixed. 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 and Boreal-Tundra species present at the start of the plot monitoring period for BCI models, and as the total relative cover of Boreal and Boreal-Tundra 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 (the southernmost limit of the boreal forest) 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 (woody, not woody), deciduousness (evergreen, deciduous), N-fixing capacity by symbiosis with N_2-fixing bacteria (fixer, non-fixer), berry-production (berry producing, non-berry producing), taxonomic family (including 36 families) 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 multivariate 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.

To characterise plots with boreal expansions only (**Table S2, S3**), 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, S3**), 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 (**Table S2, S3**). 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 & 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 net change per species (**Figure S1b**), indicating that more frequent colonisations per species generally correspond to a net abundance increase.

To identify which traits are associated with species contributing to borealization (Boreal and Boreal-Tundra 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, S3**). Continuous traits were log-transformed as species differences are better characterised on a log-scale (Bjorkman *et al.* 2018a; Westoby 1998). 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 did not 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). Therefore, even though we originally extracted data for 11 traits, only five (plant height, SLA, seed mass, leaf N and functional group) were eventually included in the species models as a result of correlations between traits and uneven sampling sizes.

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 [as gamma(0.01, 0.01)] for the dispersion parameter of the negative binomial family.

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 chain with 2,000 iterations, and 400 iterations of warm-up, with an 'adapt_delta' value of 0.8 (the average probability of accepting a posterior draw) and 'max_treedepth' of 10 (depth of the tree being evaluated in each iteration). Convergence was assessed through examination of the R_{hat} term and trace plots. Correlation plots were visualized with the 'corrplot' package (Wei & Simko 2021). In all Bayesian models, we considered an indication of statistically clear effects if the 95% credible intervals did not overlap zero.

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**). When comparing the observed BCI values with those expected by chance (i.e., null models), we found that observed values were only different to those simulated by chance (mean ± 2 SD) in 2.5% of plots. For BAI, observed values were different to those simulated in 7.4% of plots.

Within plots that had experienced boreal colonisations (i.e., 'positive-only' BCI models), mean BCI was greater at sites in Eurasia (EA) and Western North America (WNA), and were more variable in Eastern North America (ENA). BCI was lower in Greenland-Iceland (GI) than in EA (**Figure 2a**). BCI was also greater at sites that were relatively warm (**Figure 2c**), had warmed least over time (**Figure 2e**) and increased least in precipitation (**Figure 2f**), though the effect size of climate change was relatively small (**Table S3**). 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 relatively similar across regions, but they were stronger in EA compared to WNA (**Figure 2h**). BAI was greater at sites closer to treeline (**Figure 2i**), that had increased least in precipitation (**Figure 2j**) and that had lower initial boreal abundance (**Figure 2l**), though these three had relatively weak effect sizes (**Table S3**). 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**), though again the effect sizes were relatively weak (**Table S3**). All other variables in the biogeographic, climatic and local models had 95% credible intervals that overlapped zero.

Species analyses

On average, there were 2.8 and 3.2 times fewer colonisations of Boreal than Boreal-Tundra and Ubiquitous species, respectively, while Arctic species colonisations were very variable (**Figure 3a**). However, the magnitude of species abundance increases did not differ across different classes, and was highly variable for Boreal and Arctic species (**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 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 shrub *Salix arctophila* (0.87% cover change per year), and the Boreal-Tundra 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 S4**). Generally, species that were gained more frequently were also lost more often (slope = 0.66, CI = 0.59 to 0.72).

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 3.2 and 7.2 times more than forbs, respectively, in the multivariate model (**Figure 4b**), while in the univariate model only shrubs colonised 2.1 times 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 (**Table S3**). 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).

Discussion

Despite net borealization being limited and borealization rates not being different to random expectation, borealization occurred in around half of the 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 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. Boreal colonisations were more likely to occur closer to treeline (**Figure 2b, g, i, k**), highlighting the role of boreal ecosystems as a current and future source of potentially expanding species into the tundra (Lloyd *et al.* 2002). Increased boreal abundance and colonisations were more likely to occur at high elevations, suggesting that borealization is more likely in Oro-Arctic alpine regions, which have shorter distances to treeline and reduced geographical barriers to dispersal (Chan *et al.* 2024), rather than in lowland Arctic areas. 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**), although these effect sizes were relatively weak. Generally, Arctic sites with reduced climate change would be closer to the latitudinal treeline, since the Lower Arctic has experienced lower warming rates than the High Arctic (IPCC 2021; this positive relationship between latitude and warming was also present in our dataset: slope = 0.04, 95% CI = 0.01 to 0.07). 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 (Dial *et al.* 2022; García Criado *et al.* 2020; Roland *et al.* 2021). 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 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 more frequently than forbs (**Figure 4b**), possibly due to their inherent competitive advantages (Bråthen *et al.* 2021; Liu *et al.* 2018; Pajunen *et al.* 2011). 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 might indicate that the species driving borealization are generally more dynamic and thus contribute more to 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 species colonised plots 2.8 and 3.2 fewer times than Boreal-Tundra and Ubiquitous species (**Figure 3a**). This could indicate that species that are already present in local Arctic species pools (e.g., Boreal-Tundra, Ubiquitous) are better able to establish into new areas (e.g., through propagule pressure). Widespread species might be generalists and/or have broader bioclimatic niches, and could therefore increase in abundance and ultimately expand into new areas more efficiently than purely Boreal 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 species might not survive these environmental filters towards successful dispersal and establishment (Callaghan *et al.* 2004a). For instance, boreal understory shade-adapted species could struggle with greater light availability in open tundra habitats and the greater temperature fluctuations (Sanczuk *et al.* 2023, De Pauw *et al.* 2021), thus leading to reduced expansions of Boreal specialists in the tundra. Therefore, purely Boreal 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.* 2004a; 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 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 present 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 & Hollister 2012). Acknowledging that 'top coloniser' species (**Table S4**) 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. Relatedly, our null models showed that the observed values of BCI and BAI were not different from those that would be expected by chance alone, thus reflecting actual plant community dynamics. Here, we focus on borealization as one such process of community change and aim at capturing its occurrence and associated drivers.

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) migration lags of plants into the Arctic at millennial scales have been reported following deglaciation periods (Alsos *et al.* 2022). 2) 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)., 3) Some species including conifers (typically boreal species), have slow establishment rates, particularly at their northern range edges (Kroiss & HilleRisLambers 2015). 4) 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). 5) 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 species within our dataset. Thus, more standardised studies at the boreal-tundra ecotone boundary are needed to refine estimates of boreal species encroachment rates. 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 boreal-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, ecosystem functions and people living in the Arctic. 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). Simultaneously, borealization could reduce habitat quality for tundra species such as barren-ground caribou (*Rangifer tarandus groenlandicus*; Fullman *et al.* 2017), which feed mostly on lichen that could be outcompeted by shrub growth (Cornelissen *et al.* 2004). However, climate itself could be a stronger driver of herbivore community change (Speed *et al.* 2021). Increased presence of boreal plant species within the tundra could also alter nutrient cycling and reduce soil carbon storage (Gustafson *et al.* 2021; Parker *et al.* 2021; Speed *et al.* 2015), while also decreasing albedo, thus leading to further permafrost thaw and creating positive climate feedbacks via increased warming (Heijmans *et al.* 2022). Ultimately, borealization could also pose socio-economic impacts for people, for instance compromising food security through shifts in edible plants and altered migration routes for reindeer/caribou (Hupp *et al.* 2015; Rees *et al.* 2008). Overall, future research is needed to unveil the multi-faceted consequences of tundra borealization.

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Figures

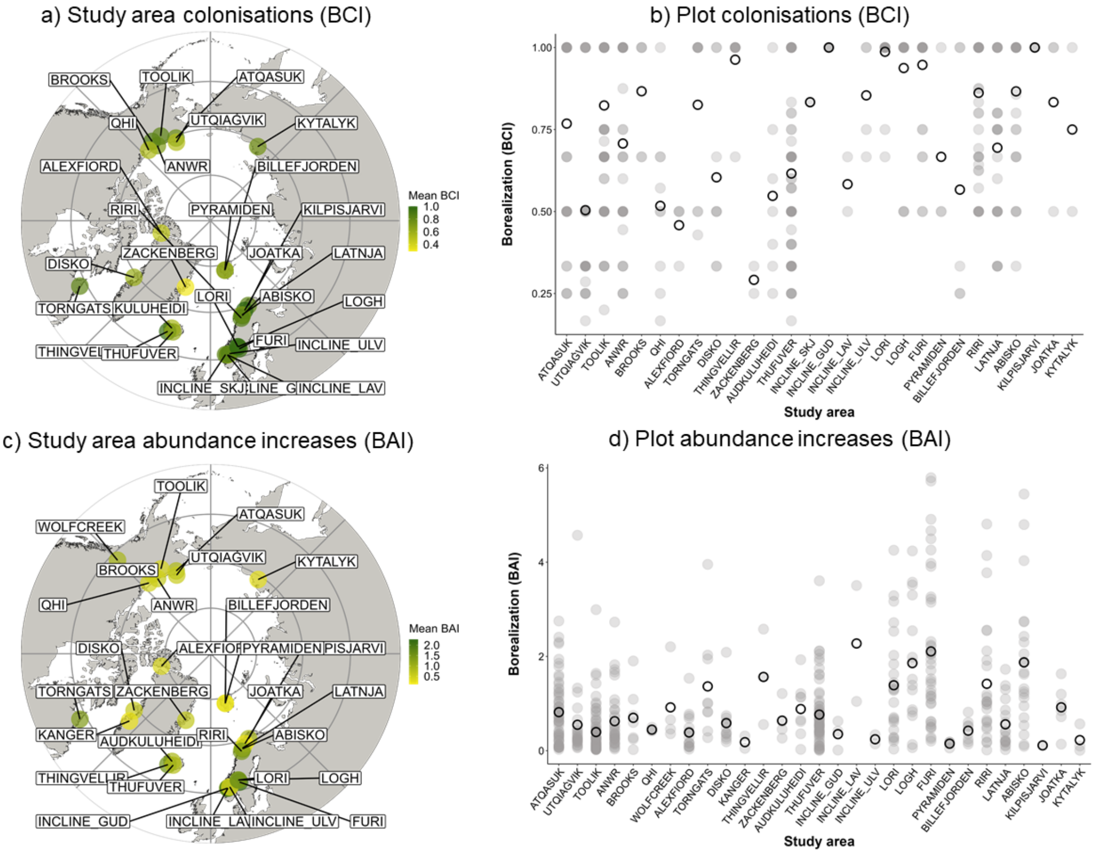

Figure 1. The magnitude of boreal plant community colonisations (BCI) and plot abundance increases (BAI) varied across the tundra. **a)** BCI estimated as the average of the plots within a study area that experienced colonisations of boreal species (BCI > 0), **b)** BCI index of those plots within each 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. Open circles 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**.

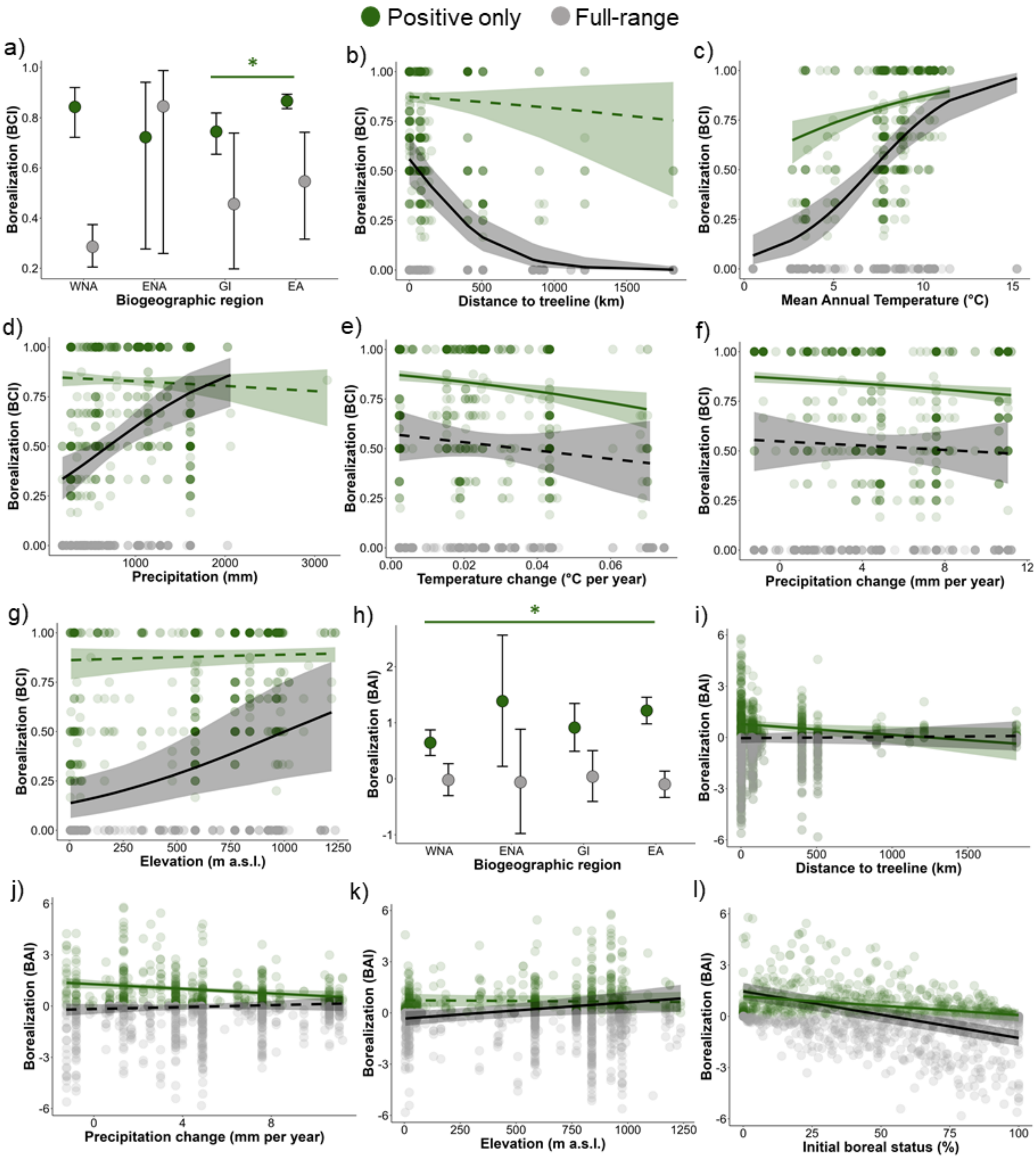

Figure 2. Borealization was associated with biogeographic, climatic and local variables across the tundra biome. Borealization was estimated using colonisations (BCI; **a-g**) and abundance change (BAI; **h-l**). As assessed using multivariate models, colonizations by boreal species were more likely 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**). Multivariate models show that 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 multivariate 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 95% credible intervals of fixed effects that did not overlap zero, and dashed lines indicate 95% 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.

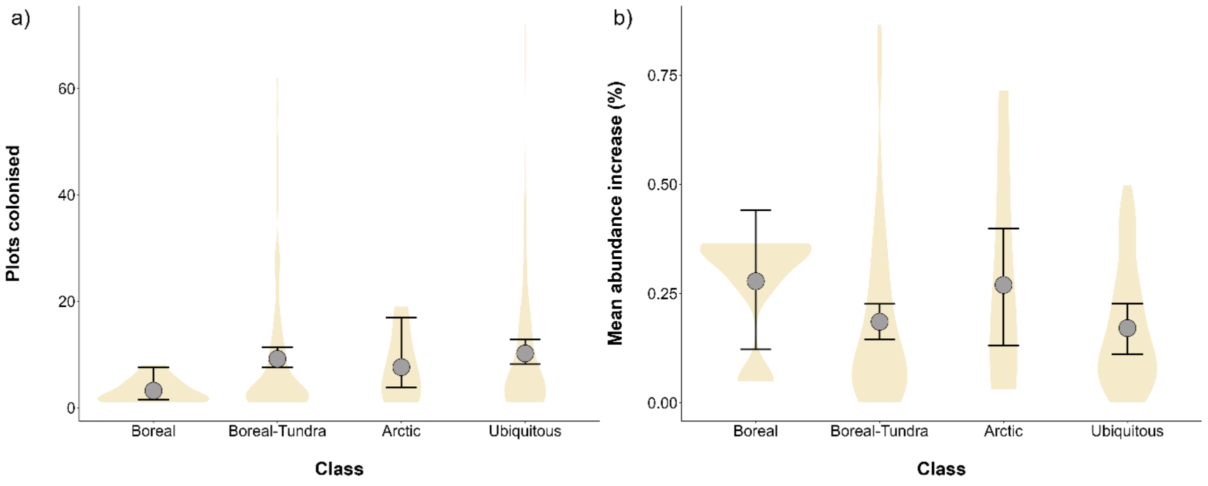

Figure 3. Model estimates at the species level, with **a)** total number of times colonising plots (model sample size = 220), and **b)** mean annual abundance increases across all plots (model sample size = 129), as a function of class. Violin plots indicate the distribution of the raw values. Points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

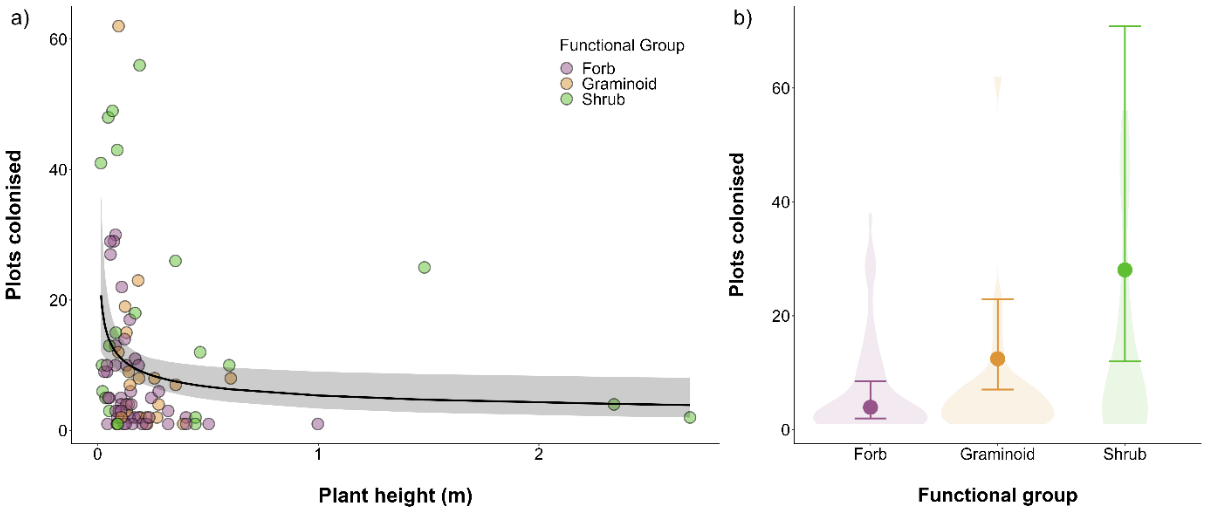

Figure 4. Colonising boreal species were shorter and more likely to be shrubs or graminoids, though shrub species spanned the full range of height values. **a)** Boreal species that were shorter colonised plots more often than taller species. Each point represents a plot, coloured according to the functional 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. Violin plots indicate the distribution of the raw values. 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.

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