Plant diversity dynamics over space and time in a warming Arctic

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Code and data availability: code will be made available in a public access repository upon publication. ITEX+ data on plant composition and abundance will be published at https://githubcom/annebj/ITEX30_VegComp. A previous version of this dataset can be accessed at http://polardata.ca/, CCIN Reference Number 10786.

Abstract

The Arctic is warming four times faster than the global average, and plant communities are responding through shifts in species abundance, composition and distribution. However, the direction and magnitude of local plant diversity changes have not been explored thus far at a pan-Arctic scale. Using a compilation of 42,234 records of 490 vascular plant species from 2,174 plots at 45 study areas across the Arctic, we quantified how species richness and composition have changed over time during a period of up to four decades (1981 – 2022), and identified the geographic, climatic and biotic drivers behind these changes. Despite plant species richness being greater at lower latitudes and warmer plots, pan-Arctic species richness did not change directionally over time at the plot level. However, 99% of the plots experienced changes in species abundance, with 66% of plots either gaining or losing species. Species richness increased most where temperatures had warmed most over time, and shrub expansion led to greater species losses and decreasing richness. Yet, Arctic plant communities did not become more similar to each other over time, suggesting that no biotic homogenisation has occurred thus far. Overall, we found that Arctic plots changed in richness and composition in all possible directions, yet climate and biotic interactions still emerged as the main drivers of directional change. Our results show a variety of diversity trends, which could be precursors of future changes for Arctic plant biodiversity, ecosystem function, wildlife habitats and livelihoods for Arctic Communities.

Introduction

Climate change is altering biodiversity patterns on Earth[1,2]. At global scales, biodiversity loss from species extinctions is the prevalent trend[3,4]. At regional scales, biotic homogenisation has been observed[5,6], while at local scales studies have shown increased turnover, but often no net richness change[7,8]. Directional species responses have been observed across temperate and tropical biomes[2,9]. However, surprisingly little is known about species responses at northern latitudes, despite Arctic ecosystems experiencing four times faster warming than the global average[10]. Plants are the foundation of Arctic ecosystems, but we have yet to quantify the effects of climate change on their abundance, richness and composition.

The direction and magnitude of Arctic plant diversity change could be shaped by multiple processes. If species migrate northward as the climate warms, we would expect a net increase in overall Arctic plant species richness[11–13]. Reduced Arctic floral diversity could also result from losses of cold-adapted species[14] that cannot cope with warming temperatures. These declines can be exacerbated by increased competition from colonising species originating from Low Arctic and boreal latitudes[15,16]. Alternatively, richness increases and decreases could balance each other out, resulting in no net richness change. Yet, the effects of these different pathways on current and future Arctic plant diversity trends remain poorly understood. Here, we quantify the direction and magnitude of Arctic vascular plant species diversity changes over time at the local level (α-diversity) and investigate which geographic, climatic and biotic drivers affect these trends.

Species richness patterns are broadly driven by climatic gradients. Macroecological theory has long established that species richness is greater at lower latitudes, which are generally warmer[17–19]. Thus, overall Arctic plant richness is expected to increase as rapid warming[10,20] leads to new warmer thermal niches becoming available to warm-adapted species. This expectation is further supported by observed climate-induced increases in vascular plant species richness across European mountaintops[21,22], whose elevational gradients mirror latitudinal Arctic gradients. Spatially, we would expect plant richness to increase at warmer, lower Arctic latitudes because of the potential influx from the species-rich boreal forest (‘borealisation’)[23–25] and the fact that the Low Arctic flora are more dissimilar to boreal flora than to the High Arctic flora[26]. Further processes contributing to plant richness change are the spread of alien species[27,28] and advancing tundra shrublines composed of tall shrub species[29–31]. While rapid warming is expected to further shift Arctic biotic communities, the direction of local plant diversity change remains uncertain[11,32], particularly since large-scale biodiversity trends do not necessarily translate into local changes in species richness[33].

Biotic interactions are another key driver of species distributions. The presence and abundance of different functional groups (e.g., graminoids, forbs, shrubs) are important attributes of plant communities, and changes in dominance of one functional group can impact others[34,35]. Climate change can also lead to shifts in the relative abundance of different functional groups[30]. For example, the phenomenon of Arctic shrub expansion has been associated with decreases in lichen, bryophyte and bare ground cover[11,32]. Favourable traits such as higher and denser canopies allow tall shrubs to outcompete shorter species for light, and deciduousness contributes to rapid resource acquisition[36,37]. Thus, the presence and abundance of non-shrub vegetation might decrease due to the shading or nitrogen depletion effect of taller shrubs[15,38]. Since the dominance of generalist and competitive species entails increased local extinction risk for rare species[39], we might expect species richness to decrease where shrub cover has increased over time.

Temporal changes in spatial dissimilarity of species composition (i.e., spatial β-diversity changes over time) are expected across the Arctic. As observed across other biomes[40], Arctic vegetation might become spatially more homogeneous (i.e., lower β-diversity) with climate change. Tundra landscapes are forecasted to become more similar to each other due to winter warming and/or the expansion of the same dominant species across sites, for instance dwarf shrubs in the High Arctic[41,42]. In fact, biotic homogenisation at the tundra-forest ecotone can be attributed to shrub expansion[43]. Yet, Arctic landscapes could also become more spatially heterogeneous due to permafrost thaw and hydrology changes, including the development of wetland plant communities[44,45]. The borealisation of Arctic ecosystems close to the treeline could also promote greater variation among Low Arctic plant communities compared to circumboreal plant communities[46]. Overall, uncertainty remains on whether Arctic plant communities will become more or less similar to each other with climate change.

Here, we quantify the direction of Arctic vascular plant diversity change through the calculation of multiple local-scale diversity metrics: richness, richness change, evenness (Pielou), evenness change, temporal turnover based on presence-absence and abundance change (Jaccard and Bray-Curtis), and species trajectories (species gains, losses and persistence). Furthermore, we identify the specific geographic (latitude, biogeographic region), climatic (moisture, warmest quarter temperature, precipitation, and their change over time), biotic (functional group composition and its change over time), and sampling variables (plot size, plot-level species richness and monitoring duration) driving diversity patterns and trends. Finally, we investigate whether vascular plant communities across the Arctic are becoming more similar (e.g., low β-diversity) over time. We use 42,234 records from 2,174 plots in 45 study areas encompassing 490 vascular plant species, monitored at different intervals over four decades (1981 – 2022, **Figure S1**) from a tundra plant community composition database (**Figure 1a**, International Tundra Experiment Plus, ITEX+). ITEX+ sites have a hierarchical structure: species composition data are recorded at the plot level, and there are multiple plots within a subsite, and multiple subsites within a study area. The 45 long-term monitoring study areas capture most of the variation in temperature and precipitation across the Arctic tundra (**Figure 1b**) and represent diverse assemblages of tundra functional groups (**Figure 1c**).

We address three main research questions:

1) How has Arctic vascular plant diversity changed over the past four decades?

We expect an overall increase in plot-level richness (α-diversity) over time across the Arctic due to colonisations from species with warmer thermal niches, reflecting spatial patterns such as the latitudinal biodiversity gradient[47] and leading to a decrease in plot-level evenness.

2) Which are the main geographical, climatic, and biotic factors underlying these diversity changes?

We expect greater plot-level richness increases in warmer plots and at lower latitudes, where Low Arctic flora are more differentiated from boreal flora than from High Arctic flora. We hypothesise that increases in shrub abundance are associated with decreases in non-shrub vascular plant richness.

3) Are vascular plant communities across the Arctic becoming more compositionally similar over time?

As sites warm up, they will become available to thermophilous species with lower cold-tolerance and better dispersal capacities[48]. This could lead to an increased pool of boreal and Low Arctic species with advanced dispersal and adaptation capacities above the current treeline[24,41,42]. We hypothesise that the infilling of warmer thermal niches by the same southern species will lead to biotic homogenisation of plant communities (measured as spatial β-diversity through time), as per projections[42].

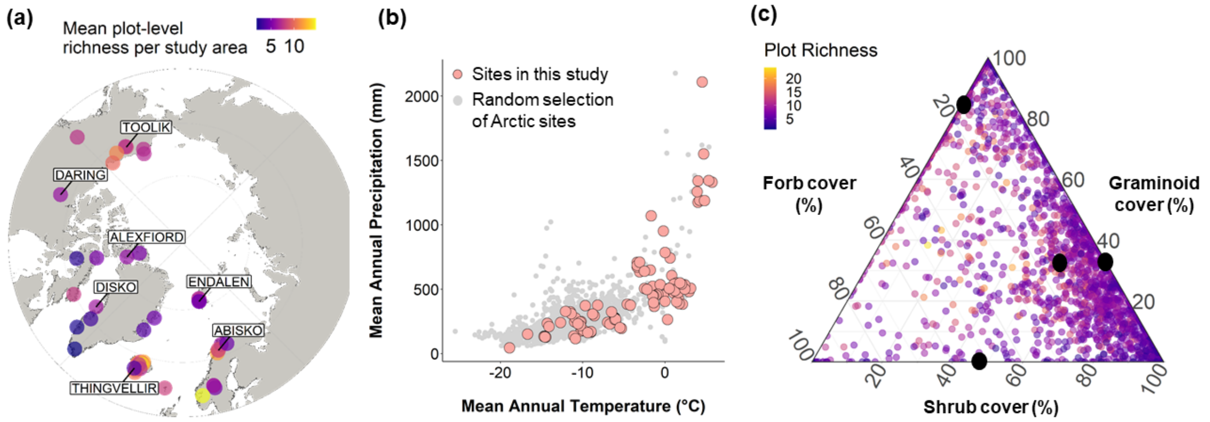

Figure 1. Representation of our database within the geographical, climatic, and biotic space. a) Distribution of study areas, coloured according to mean plot-level richness per study area (*n* = 45). This mean calculation is done for visualisation purposes only, with all the analyses and estimates presented elsewhere using individual plot-level richness, unless stated otherwise. A few of the 45 study areas are labelled for reference across our latitudinal gradient of 20.78 degrees. Polar projection with a southern limit of 57 degrees latitude. **b)** Subsites (*n* = 115) included in this study as a function of their climatic space. Background grey points represent a random sample selection of 1,189 locations across the Arctic for which climatic data were extracted. The subsites included in our study cover an extensive gradient of the climatic conditions found across the Arctic. **c)** Relationship between mean cover (calculated as average cover per functional group over the entire period per plot) of the different functional groups per plot (*n* = 2,174). Species-rich plots had greater forb cover, while greater graminoid cover was associated with species-poor plots. All functional groups were negatively correlated with each other, and particularly when shrub cover was higher, the cover of graminoids and forbs was lower. Points represent plots and are coloured according to mean plot species richness over time. Bigger black

points indicate mean plot cover for each functional group marked on each axis, and the black point inside the ternary plot indicates the mean cover per plot of all functional groups.

Results

No directional trend in changes in species richness across the Arctic. Spatial plot-level richness (calculated as average richness across all years per plot) was greatest at lower latitudes, with nearly one species fewer per every 5° increase in latitude (slope = -0.03 species/degree, 97.5% CI = -0.05 to -0.01; **Figure 1a, S2a, b**). Richness was also greater at warmer plots, with one species gained every 2°C increase in warmest quarter temperature (slope = 0.06 species/°C, 97.5% CI = 0.03 to 0.1) and in plots with greater forb cover and lower graminoid cover (**Figure 1c, Table S1**). However, plot-level richness change over time was not statistically different from zero (slope = 0.0019 species/year, 95% CI = -0.0005 to 0.0042; **Figure 2b, Table S1**).

Species richness change was not related to latitude (**Figure 2a, Table S1**), but richness increased where temperature had increased the most (**Figure 2c**, **Table S2**). However, after accounting for other covariates (moisture, change in functional group and precipitation, and sampling variables, see **Table S1**), this relationship was no longer statistically significant (**Table S2**), suggesting combined effects of different drivers. There was no relationship between mean plot species richness and species richness change over time (slope = -0.002 species change/species, 95% CI = -0.005 to 0.002). Mean evenness (Pielou) across the Arctic was 0.7 [data bounded by 0 – 1]. Evenness was greater at higher latitudes and in more diverse plots with high forb cover and low shrub cover, and in Western North America relative to other regions (**Table S1**). Overall, evenness did not change over time (**Table S3**), but increases occurred mostly in plots where forb and graminoid cover increased and shrub cover decreased over time (**Table S1**). Plots that were more diverse and more even experienced fewer plot-level species gains and losses (**Figure S3**).

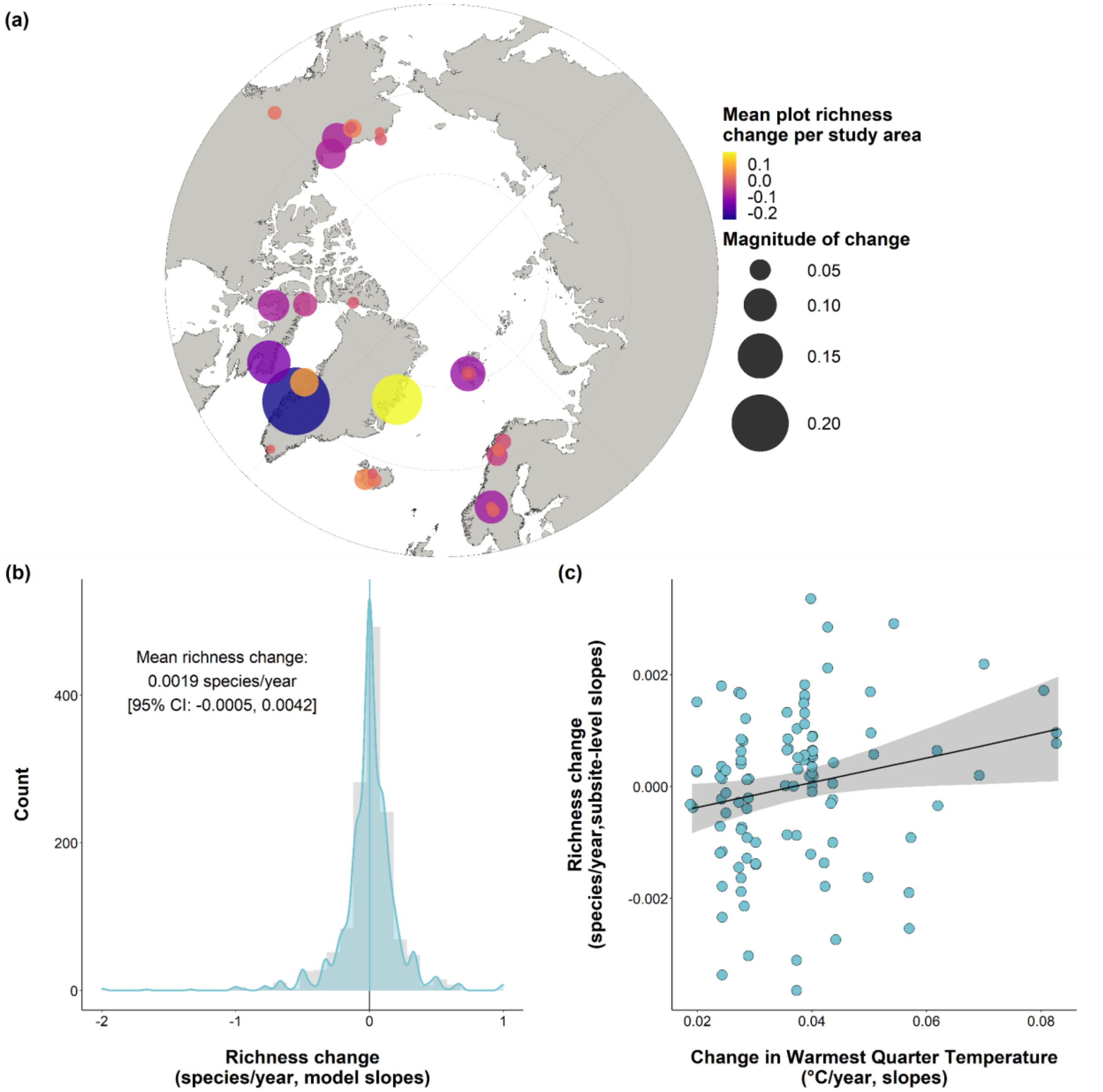

Figure 2. There was no directional change in species richness across the Arctic. a) Richness change values calculated as the mean slope of richness change across all plots in each of the 45 study areas. This average is done for visualisation purposes only, with analyses and estimates of richness change elsewhere calculated at the plot level. Points are coloured according to their richness change value (including positive and negative values) and sized according to their magnitude of richness change (in absolute terms). Polar projection with a southern limit of 57° degrees latitude. **b)** Mean richness changes across all plots that were surveyed at least twice (*n* = 1,387 plots), calculated as the slope of richness over time per plot. The blue line represents mean richness change and its 95% credible intervals, which is virtually indistinguishable from the zero line (in black). Histogram bin width is 0.1. **c)** Richness increased at subsites where warmest quarter temperature increased the most over time. Points represent richness change slopes at the subsite level (*n* = 106), the black solid line indicates the predicted model fit and bands show the 95% credible intervals. All analyses are Bayesian hierarchical models.

Changes in species composition. Arctic plots experienced a mean temporal turnover of 0.21 (Jaccard) and 0.34 (Bray-Curtis) [data bounded by 0 – 1] between 1981 and 2022, reflecting presence-absence and abundance-related turnover at the plot level, respectively (**Figure 3a**, **b**). Greater presence-absence temporal turnover (Jaccard) was associated with colder plots, regions with stronger warming trends, and species-poor plots (**Figure 3a**, **b**). Conversely, greater abundance-related temporal turnover (Bray-Curtis) was related to species-rich plots and regions with weaker warming trends (**Figure 3b**, **Table 1**). There were substantially more species persisting in plots over time (mean = 5.49 species per plot; 64%) than species gained (1.84; 19%) or lost (1.67; 17%) across plots (**Figure S4**). Proportions of species gained, persisting and lost were similar across functional groups, and to overall database composition (**Figure S5**; $p > 0.05$ for all groups in two-proportion z-test, see **Table S4** for top species per trajectory).

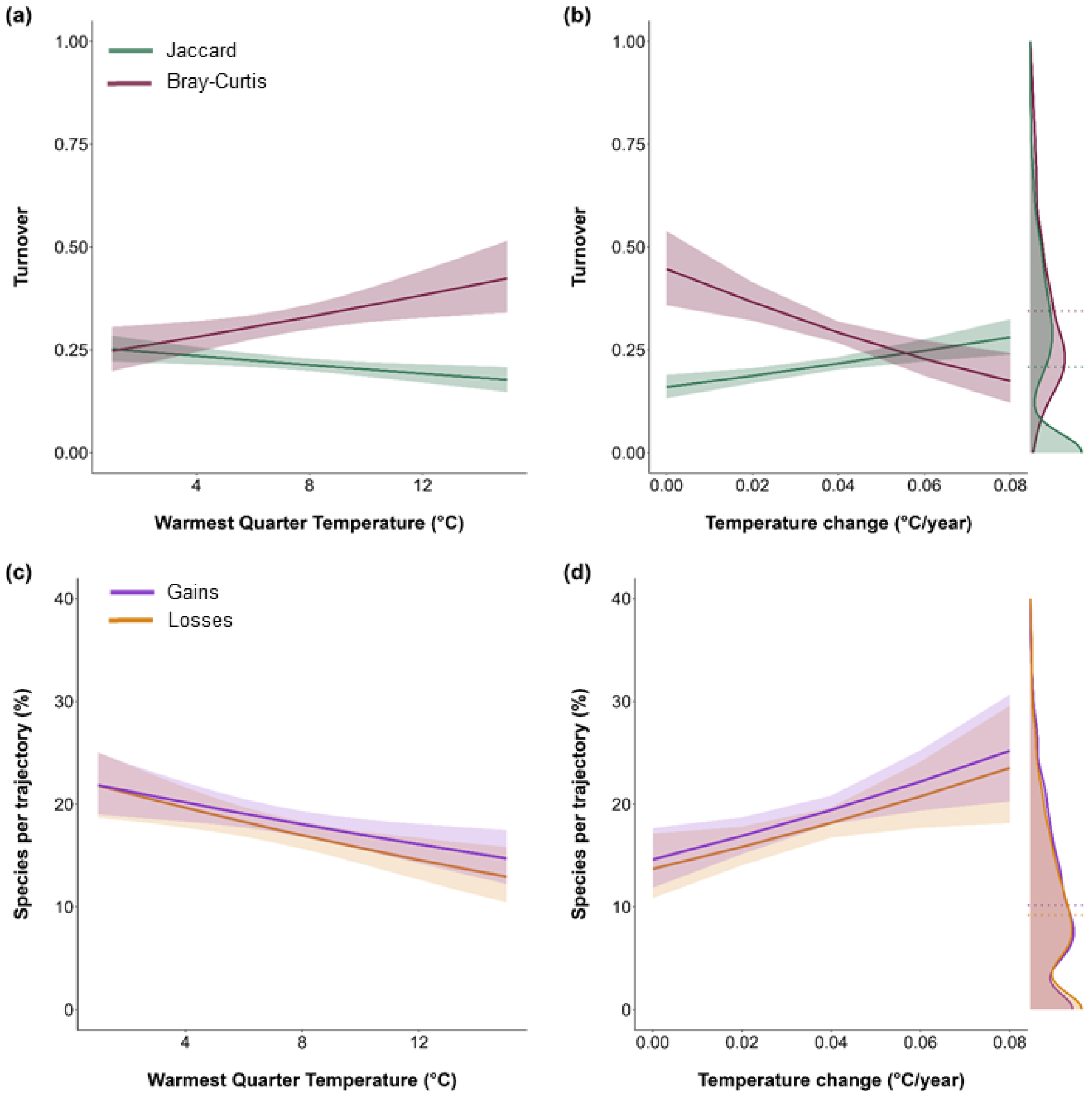

Figure 3. Both local climate and climate change over time influenced species' temporal turnover and trajectories. a) Relationships between climate (mean warmest quarter temperature, MTWQ) and two temporal turnover metrics: Jaccard (presence-absence turnover) and Bray-Curtis (presence-absence and abundance turnover). **b)** Relationships between temperature change over time (slopes from linear models) and the two turnover metrics. Density plots reflect the distribution of the Jaccard and Bray-Curtis values across all Arctic plots that were surveyed more than once (*n* = 1,387). Dotted lines indicate mean values overall. 612 (44.1%) plots did not change at all in terms of presence-absence turnover (Jaccard) and only 9 (0.6%) plots did not change at all when considering both presence-absence and abundance turnover (Bray-Curtis). **c)** Relationships between MTWQ and species proportion for each trajectory (species gained and lost, persisting species are not displayed). **d)** Relationships between temperature change over time (MTWQ) and species proportion for each trajectory. Lines represent predicted model fits and bands show the 95% credible intervals. Density plots reflect the distribution of the proportion of gains and losses across all Arctic plots (*n* = 1,387). Dotted lines indicate mean values per trajectory. All analyses are Bayesian hierarchical models.

Climate and climate warming influenced species trajectories. There were more persisting species at warmer and drier plots, and more plot-level species losses and gains in colder plots (**Figure 3c**). Stronger warming trends were associated with reduced plot-level species persistence and higher plot-level losses and gains over time (**Figure 3d**). Regional climates across the Arctic varied widely in their annual coldest quarter temperatures, but less so in their warmest quarter temperatures (MTWQ, **Figure S6a**). All subsites experienced MTWQ increases (**Figure S6b**), and 87.6% of subsites experienced mean annual precipitation increases over time (**Figure S6c**). The magnitude of warming over time was greater at northern latitudes (slope = 0.00033°C/year, 95% CI = 0.00018 to 0.00047).

Plot-level shrubification corresponded with decreasing species richness. Decreases in richness were more common in plots where shrub cover increased over time (**Figure 4a**), but this relationship was not dependent on the baseline (i.e., initial) shrub cover (**Figure 4d**, **Table S7**). Richness increased over time with increasing forb and graminoid cover (**Figure 4b**, **c**). Similarly, species persistence was related to decreasing forb and increasing graminoid cover over time. There were more species losses where shrubs had increased and graminoids had decreased, and more species gained where forbs had increased (**Figure 4e**, **f**).

Most plots were dominated (i.e., cover was > 50%) by shrubs (*n* = 1,170, 53.8%), followed by graminoid-dominated plots (689, 31.7%), plots where none of the functional groups were clearly dominant (202, 9.3%) and forb-dominated plots (113, 5.2%). Similarly, mean cover across plots was greater for shrubs (50%), followed by graminoids (37.4%) and forbs (12.6%, **Figure S7**). Forb cover did not directionally change over time on average across the Arctic, but shrub cover marginally increased and graminoid cover decreased over time (**Table S5**, **S6**). Species-rich plots had higher forb cover and lower graminoid cover (**Table S1**). See **Supplementary Results** for the effects of geographic and sampling design variables.

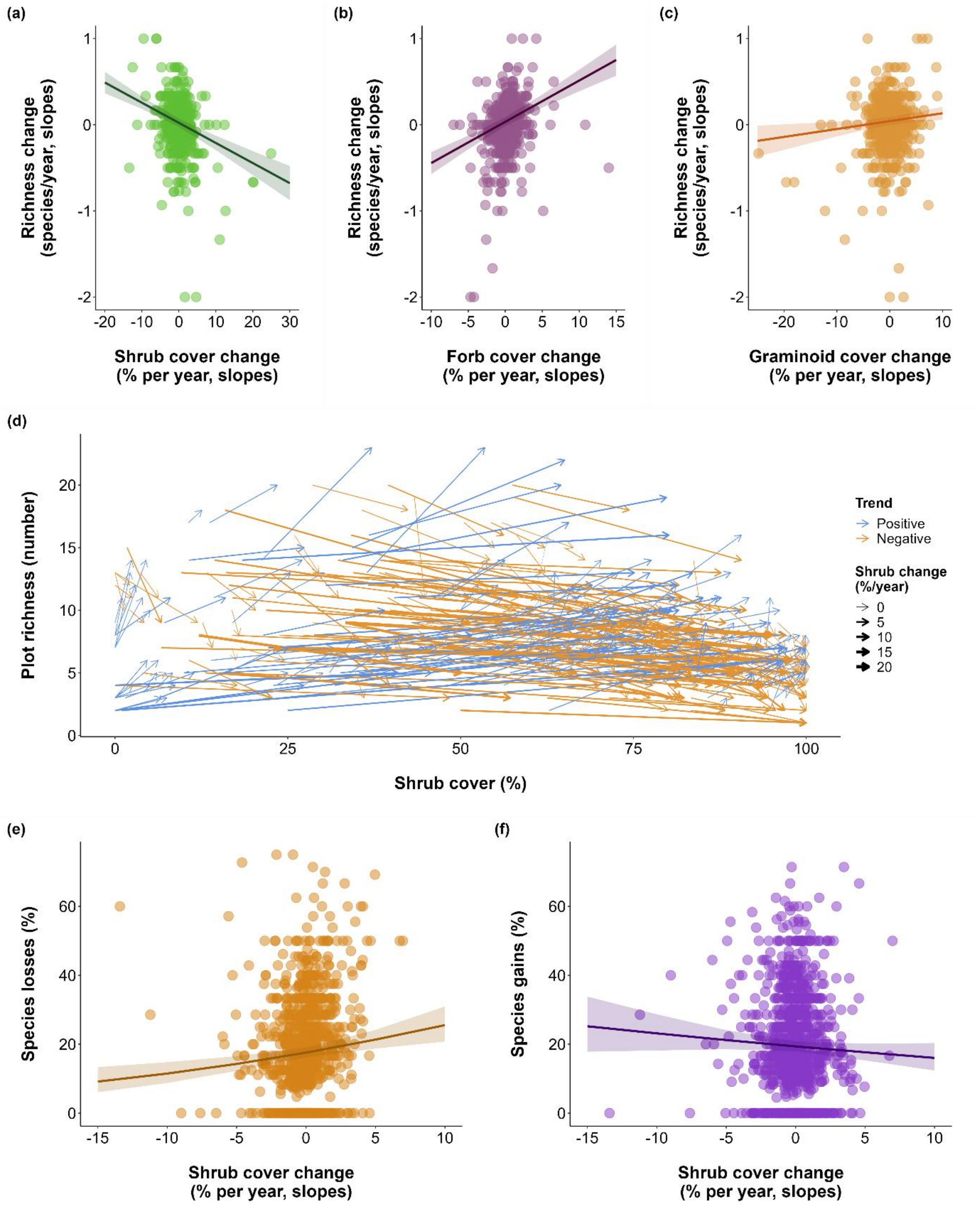

Figure 4. Shrub cover influenced species richness change and trajectories. a) Richness decreased as shrub cover increased over time, but increased when **b)** forb and **c)** graminoid cover increased. Scatterplots represent richness change over time as a function of changes in cover of shrubs, forbs and graminoids. Points represent slopes of linear models of change in richness and in functional group change per plot over time. Lines represent predicted model fits and bands show the 95% credible intervals (see **Table S1** for full model structure and summary statistics). **d)** Plot richness change was related to shrub cover increases over time, particularly at higher values of shrub cover.

Each arrow connects the first and last monitoring point for each plot, with the arrow head pointing at the end time point. Arrow colours indicate the relationship between shrub cover increase and plot richness. 'Positive' indicates that plot richness increased as shrub cover increased. 'Negative' indicates that plot richness decreased as shrub cover increased. Arrow thickness indicates the magnitude of shrub change over time. Only plots where shrub cover increased over time are displayed (*n* = 432). **e)** Increases in shrub cover over time were associated with increased species losses and **f)** decreased species gains (though this effect was non-significant, see **Table S1**, **S2**). Points represent slopes of linear models of change in shrub cover and the proportion of species per trajectory and plot. Lines represent predicted model fits and bands show the 95% credible intervals. All analyses are Bayesian hierarchical models.

We found no indication of biome-wide biotic homogenisation across the Arctic. Our ordination analyses did not indicate any signs of biome-wide biotic homogenisation or heterogenisation. Subsites did not become more or less similar to each other over time as they shifted in their composition in all possible directions, and their location in the ordination space was broadly driven by latitude (**Figure 5a**, **b**). There were similar distances to centroid between start (i.e., baseline) and end (i.e., final) timepoints per subsite both for Jaccard (mean ± SD start: 0.66 ± 0.02, end: 0.66 ± 0.02) and Bray-Curtis (start: 0.65 ± 0.04, end: 0.65 ± 0.04) (**Figure 5c**, **d**, **Figure S8**; $p > 0.05$ in ANOVA for all β-diversity metrics). Mean shifts in distance between timepoints per subsite was 0.039 ± 0.036 (Jaccard) and 0.04 ± 0.03 (Bray-Curtis, **Figure 5e**).

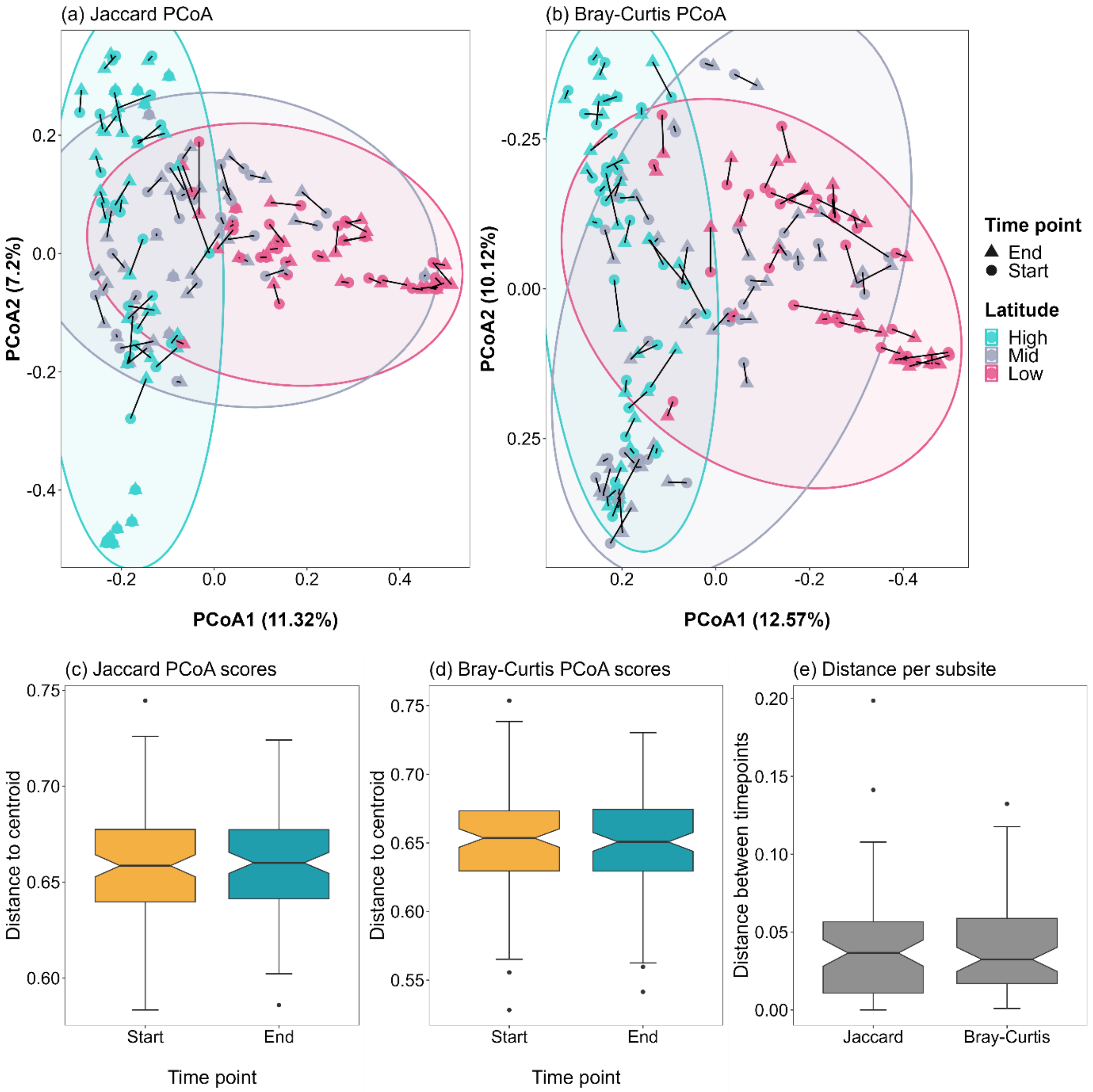

Figure 5. Subsites showed no homogenisation or heterogenisation over time across the Arctic. We calculated temporal change in spatial turnover (β-diversity) between the start (i.e., baseline) and end (i.e., final) time period for all subsites. Principal Coordinate Analyses (PCoAs) are shown with the **a)** Jaccard and **b)** Bray-Curtis β-diversity metrics. Triangles represent the start time point and circles represent the end time points for all subsites, joined by a line per subsite indicating the start and end time point. Points are coloured according to latitude (represented as high, mid and low latitudes based on the 33.3% quantiles of latitude values). Enclosing ellipses are drawn around subsites following the same colour scheme, and are estimated using the Khachiyan algorithm. Boxplots show the mean distance to centroid for all start subsites versus end subsites for **c)** Jaccard and **d)** Bray-Curtis scores derived from PCoAs. **e)** Mean distances in ordination space between timepoints (start versus end) for all subsites, calculated as Cartesian coordinates. These values show how much plant communities have changed in composition and abundance.

Discussion

Vascular plant species richness was greatest at lower latitudes and in warmer plots of the Arctic (**Figure S2**, **Table S1**). Despite temperatures rapidly increasing over the past few decades (**Figure S6b**), we did not find evidence of directional richness change over time across plots (**Figure 2b**). Yet, richness increased where subsites had warmed the most (**Figure 2c**, **Table S2**). Plots across the Arctic experienced changes in community abundance and composition (**Figure 3a**, **b**). Species trajectories were associated with climate, with more species losses in colder plots that had warmed the most (**Figure 3c**, **d**). Increases in shrub cover over time were related to decreases in richness and evenness, and greater species losses (**Figure 4**, **Table S1**). We found some community resistance to rapid Arctic warming, with fewer species losses in plots that were more diverse and even (**Figure S3**). We observed no signs of Arctic-wide subsite homogenisation as shown by temporal changes in spatial dissimilarity of species composition (**Figure 5**, **S8**). Our results suggest no directional vascular plant species richness change so far despite substantial shifts in community composition across the Arctic.

Contrasting trends of richness change across the Arctic. The latitudinal diversity gradient extends across the Arctic, with greater plant species richness in low latitudes and at warm sites (**Figure S2**, **Table S1**), in agreement with global latitudinal[17,19] and elevational gradients[49,50]. Yet, despite rapid Arctic warming, overall plot richness (α-diversity) had not changed directionally across the Arctic over time (0.019 species/decade, **Figure 2b**), showing the potential for plant communities to change in a variety of directions. Our results are consistent with the polar terrestrial parts of global richness change studies[7,51,52], reflecting similar numbers of species losses and gains across plots (**Figure S4**). While richness change was not related to latitude, richness increased where temperatures had warmed the most (**Figure 2c**). However, after accounting for other variables this relationship was no longer statistically clear (**Table S1**, **S2**), suggesting covariance between temperature change, functional group composition change and sampling variables. Still, plant communities experienced substantial turnover over time (**Figure 3**), which could hint at future richness change[53]. Arctic richness increases could result from a combination of different sources of new biodiversity including: boreal species migrating into the Low Arctic[24,54,55], Low Arctic species moving towards the High Arctic, and plot colonisations by tundra plants already present in local species pools (often referred to as ‘hidden’ or ‘dark’ diversity)[56,57]. A combination of these pathways is likely to contribute to future Arctic plant composition change.

Climate and functional composition influenced diversity change. Climate played a mediating role in species trajectories over time. A greater proportion of species persisted locally in warm and dry environments, while there were proportionally more species losses in cold plots (**Figure 3c**). Interestingly, species losses were more frequent at plots that warmed most (**Figure 3d**). This could be due to cold plots experiencing greatest warming, cold-adapted species not coping with warming, or thermophilisation, if warm-adapted species displace those adapted to colder niches[48,58]. Indeed, climate is a key driver of plant diversity, community composition and species distributions[59–61], and both cold and warm tolerance might be equally important for the survival of Arctic plants[62].

Plant diversity declines have been observed in experimental settings at the local scale[63] and projected by modelling studies at the regional scale, which predicted a decline in Arctic-alpine plant species richness of 15-47%, with endemic plants being particularly threatened with extinction[14]. However, we found that the majority of species thus far (mean = 64%) persisted across plots (**Figure S4**). Plots with high species richness and more even communities showed the greatest resistance to change, with fewer species losses and gains (**Figure S3**). This result could also be influenced by species gains and losses being limited by species pool sizes, with gains and losses being proportionally greater at species-poor plots. Species pool sizes may also explain greater abundance turnover in lower, warmer latitudes and greater presence-absence turnover in colder plots (**Figure 3a**). Overall, greater community resistance could be linked to the reduced extinction risk derived from greater diversity and lack of species dominance[39,64].

Shrubification was a main component of richness and compositional change (**Figure 5**, **Table S1**). Shrub expansion has been widely reported[11,61,65], and we found a marginally significant increase (i.e., the credible intervals overlapped zero) in Arctic shrub cover at the plot scale within the ITEX+ dataset (**Table S6**). Where shrub cover increased over time, plots experienced greater species losses, leading to decreases in species richness and evenness (**Figure 4**, **Table S1**). Lower species richness has been observed with greater shrub cover spatially[15,16], and our Arctic-wide results corroborate site-level reports that increasing shrub cover over time may lead to less diverse plant communities and the displacement of less competitive species[38,66,67]. Conversely, both increasing graminoid and forb cover are associated with increased richness over time, and increasing graminoid cover was related to fewer species losses (**Figure 5b**, **c**, **Table S1**). Graminoids were more likely to persist than forbs (**Table S1**), perhaps because graminoids are good competitors that can displace shallow-rooted forbs where they both co-occur due to their deeper root networks, faster nutrient uptake and greater height[68–70]. Overall, our findings suggest that shrubs, and to a lesser extent graminoids, out-compete other groups, especially forbs, likely due to their often relatively more competitive traits[70,71].

It was not possible to include non-vascular plants (bryophytes and lichens) in our analyses due to their inconsistent recording across plots[72], but their influence on vascular plant dynamics cannot be discounted. Bryophytes can suppress vascular plant regeneration[73], while lichens have a strong buffering effect on microclimate extremes, and can thus mitigate further shrubification[74]. Therefore, plots that were initially more dominated by non-vascular plants might be more resistant to vascular plant colonisations, which could explain temporal lags in richness change dynamics. It remains a priority to expand non-vascular plant surveys to obtain a comprehensive view of plant diversity change and biotic interactions among functional groups.

Resistance to change reflects multiple ecological processes. Neither biotic homogenisation nor heterogenisation (calculated as temporal changes in spatial dissimilarity) have occurred for Arctic plant communities thus far (**Figure 5**). Homogenisation has been forecasted for High Arctic vegetation[41,42], and there was an indication that northern subsites had experienced more consistent species replacement (**Table S1**), but overall subsite change happened in all possible directions across the Arctic (**Figure 5a**, **b**). These findings support the observed global decoupling of compositional and richness change[7,8], with more evident temporal turnover than directional Arctic richness change. One clear consequence of this temporal turnover is the increase in tundra plant community height over time due to the immigration of taller species[71]. Continued compositional change is likely to lead to additional shifts in plant traits and the functioning of Arctic ecosystems.

Our results demonstrate certain resistance of Arctic plant communities to diversity change (**Figure 2b**, **S3**) despite continued warming. However, future research is required to determine whether tundra ecosystems are indeed exhibiting resilience to warming[75]. Other processes that could contribute to a lack of detected diversity change include: 1) some of the same species being both lost and gained across plots over time due to stochastic dynamics (**Table S4**), 2) slow colonisation rates and extinction lags[76] in these communities of long-lived perennial species, 3) the underlying influence of high intraspecific trait variability on species adaptation[77], 4) priority effects causing heterogeneity in species responses[78], 5) herbivore browsing counter-acting vegetation change[79], 6) the buffering effect of microclimate heterogeneity on macroclimatic change[13,80], and 7) the effects of longer growing seasons due to earlier snowmelt[81]. A better understanding of the underlying mechanisms that drive biodiversity change will be key to identifying future rates and hotspots of change under accelerating warming[55,56]. Although macroclimate regulates species richness and community composition, baseline climate context dependencies can affect species responses[82], while varied topography, microclimate and nutrient limitation could mediate ecological responses and buffer against climate change impacts[83–86]. Thus, the integration of micro- and macroclimate, together with other small-scale environmental variables, is an essential next step to better identify the mechanisms behind Arctic plant dynamics.

Our findings suggest no consistent vascular plant richness change to date despite the Arctic experiencing the greatest rates of climate change on Earth. In contrast, species in the tropics are experiencing slower rates of climate change, but greater magnitudes of biotic change[9]. This is possibly due to tropical species having narrower thermal niches than Arctic species[2,9], and having a broad thermal niche might slow Arctic species' responses to climate change. Thus far, composition and richness have changed in different ways and directions across the Arctic, thus showing a strong influence of site idiosyncrasy on compositional trends. However, climate and biotic interactions have influenced species trajectories, with species richness increasing where temperatures increased most and decreasing where shrub cover increased the most over time. Our results show a variety of diversity trends, which could be precursors of future changes for Arctic plant biodiversity, ecosystem function, wildlife habitats, and livelihoods for Arctic Communities.

Methods

Plant composition data. We extracted composition and abundance data from the International Tundra Experiment (ITEX+) database[87,88]. Our dataset was composed of 42,234 unique records from 2,174 plots within 155 subsites distributed across 45 study areas encompassing 490 vascular plant species, recorded during different intervals over the past four decades (1981 – 2022) across the Arctic. All ITEX sites have a hierarchical structure: species abundance and composition data are recorded at the plot level, and there are multiple plots within a subsite, and generally multiple subsites within a study area. 'Study areas' indicate general regions ranging in size from several hundred square metres up to tens of kilometres. 'Subsites' are smaller regions, or clusters of plots, within larger study areas, either located in different habitat types or created as blocks of plots within study areas, and 'plots' are the smallest spatial units, nested within subsites and study areas.

Plots range in size (i.e., surface area) based on the plant species community of interest and landscape characteristics[87,89] (mean plot size = 0.57 m^2, range = 0.048 to 1 m^2). There is an average of 48 plots per study area (range = 5 to 276), 14 plots per subsite (range = 1 to 87) and 3 subsites per study area (range = 1 to 11). We use the terms 'plant communities' or 'sites' when referring more generally to groups of Arctic species at any scale or resolution. Plots were monitored over different periods during four decades (**Figure S1**), with a mean study duration of 8 years (range = 1 to 28), a mean of 3 monitoring time points per plot (range = 1 to 11) and a mean time between surveys of 5 years (range = 1 to 26).

For data cleaning (taxonomic verification, input errors), we followed the same protocol as Bjorkman et al. (2018)[71]. Additionally, we retained only Arctic and subarctic plots in the Northern Hemisphere (> 60° latitude). We kept plots that had consistent sampling methods and plot sizes over time. We retained data for vascular plants only (shrubs, graminoids and forbs) since non-vascular plants were not recorded consistently across study areas. We defined biogeographic regions as Eurasia, Greenland-Iceland, Eastern North America and Western North America according to glaciation history[90,91]. We kept only plots whose surveyed area was ≤ 1m^2 in order to ensure comparable richness values across plots, given that plant species richness tends to increase with plot size according to the species-area relationship[92]. Our database contained 2,174 plots, out of which 787 plots (36.2%) had only been surveyed once (and thus were only included in spatial analyses) and 1,387 (63.8%) plots were surveyed more than once (and thus were used for both spatial and temporal analyses). Of all the plots that were surveyed more than once, 35.3% were surveyed twice, 21.5% were surveyed thrice, 19.7% were surveyed four times, 23.3% were surveyed five or more times, and 0.5% were surveyed ten or more times.

Since plant records were surveyed by different methods, we kept those that were convertible to percentage cover: point-framing with and without X-Y grid coordinates and cover-equivalent records (e.g., Braun-Blanquet). We kept all types of point-framing data (top hit, top-bottom hits, all hits) since values of overall richness were similar across methods (**Figure S9**). We compared data with hit order information and found that top and top-bottom and all values were very similar, and so were point-framing data with and without coordinates (**Figure S9**). We converted all values to relative cover (0 – 100%) to ensure consistency across survey methods (**Figure S10**). See **Supplementary Methods** for a detailed account of data cleaning and cover conversion.

We calculated functional group proportion in each plot-by-year by adding up the total cover of species within a functional group (shrubs, graminoids, forbs), so that the total vascular plant cover was 100% in each plot-by-year. We also calculated the proportion of functional group per plot by averaging the proportion of functional group cover across all years in a plot. We use this metric as an indication of the extent to which a functional group covers a plot, and refer to it as ‘greater’ or ‘smaller’ cover. Finally, we calculated functional group change over time by adding up cover values of all species per functional group and year and fitting linear models of cover over time per plot and per functional group separately. These slopes (mean annual values of functional group change) were used as fixed effects in subsequent analyses models (**Table S1**). We did not consider in the models those functional groups which were not present neither at the start nor at the end of the monitoring period for a given plot. We use this metric to indicate the degree to which functional group cover had changed over time in each plot, and refer to it as ‘increasing’ or ‘decreasing’ cover over time.

Climate data. We extracted, at the subsite level, data from long-term climatologies at CHELSA (version 1.2.1)[93] on mean annual temperature, mean temperature of the warmest quarter (MTWQ) per year, mean temperature of the coldest quarter (MCQT) per year and mean annual precipitation (MAT, hereafter ‘precipitation’). Upon examining correlations between the three temperature variables, we found that most were correlated with each other. Thus, we used only MTWQ (hereafter ‘temperature’) as it best represents the growing season conditions and might be more directly related to the biodiversity patterns of interest explored here[9]. Additionally, we extracted time series of the mean daily mean air MTWQ per year and annual precipitation amount during the period 1979 – 2013.

Biodiversity metrics. Richness was defined as the total number of species co-occurring in a plot. We refer to ‘richness change’ as changes in richness over time, including increases, decreases and no change trends. Temporal turnover was defined as the replacement rate, in terms of species composition, within a focal plot and between the starting (baseline survey) and the ending (last resurvey) year of the time period covered by the focal plot. We computed the Jaccard (based on presence-absence only) and Bray-Curtis (which considers both presence-absence and abundance change) indices. Both metrics were calculated with the ‘betapart’ package in R[94]. Evenness defines the relative abundance of different species, with high evenness indicating similar abundances of species, and low evenness indicating varying abundances. It is based on Pielou’s J, calculated as $H/\log(S)$, where H is Shannon’s diversity index and S the total number of species[95].

We considered species locally ‘lost’ if they were originally surveyed in a plot, but were not present in the last resurvey. Similarly, local ‘persisting species’ are those that were present at both the starting and ending year of the monitoring period. Species ‘gained’ are those absent during the baseline survey but occurring in the last resurvey. These species trajectories were only calculated for plots with at least two sampling timepoints and that had been monitored for longer than four years.

Statistical analyses. We employed a Bayesian framework for all analyses. We used the software and programming language R version 4.1.0[96]. Models were fitted using the 'brms' package[94] and ran for as many iterations as necessary to achieve convergence, which was assessed through examination of the R_{hat} term and trace plots. We fitted three main types of models: spatial, two time-point and temporal (**Table S1**). Spatial models refer to current biodiversity metrics across space, with one unique value of the response variable (richness, evenness) measured at the last monitoring timepoint. Two-time point models use a response variable that has been derived from two points in time, with a single value providing the measure of change (temporal turnover via Jaccard and Bray-Curtis, species losses, gains, and persisting species). Temporal models reflect metrics whose response variable had multiple values over time, and at least start and end values (richness change, evenness change, models derived from the spatial homogenisation over time analyses). For each response variable, we fitted several models (geographical, climatic, functional group composition, change over time model, plot change over time, subsite) depending on the level at which the covariates affected the response variable, in order to avoid collinearity and obscuring patterns between fixed effects (**Table S1**). We used a hierarchical modelling approach by including a subsite random effect (as random intercepts) to account for non-independence of plots within subsites.

For temporal models (i.e., richness change and evenness change), we followed a two-step modelling approach to examine biodiversity metrics over time. First, we calculated change over time by fitting linear models of richness and evenness per plot with sampling year as the fixed effect (one linear model per plot). Then, we extracted the slopes of change over time per plot and used them as a response variable in a second set of models to test the relationships between putative drivers of temporal diversity change which were measured at the plot- or subsite-level (**Table S1**). We calculated functional group change over time by fitting linear models of functional group cover over time per plot. These slopes (mean annual values of functional group change) were used as fixed effects in several models (as shrub % change, graminoid % change and forb % change, **Table S1**). We calculated change over time in temperature and precipitation by fitting linear models of yearly climatic values over time, and used the slopes per plot as the climate mean annual as fixed variables in the models (as MTWQ and precipitation change, **Table S1**). Thus, multiple plots in the same subsite had the same climatic change values, which was accounted for with the inclusion of a subsite random effect in the models.

For all temporal metrics, we retained those plots with a minimum of two sampling points. To obtain the mean richness and evenness change estimate across the tundra, we fitted high-level models of richness and evenness per year over time and included nested random slopes per plot within the subsite (**Table S3**). In these two models, the year covariate was centred as needed to achieve model convergence. To understand the effects of increasing shrub cover on richness, we modelled richness change as a function of shrub cover change and its interaction with starting shrub cover (**Table S7**). To understand whether our temporal turnover versus richness models reflected a priori relationships, we compared them with null models.

All models included a set of relevant sampling design variables to account for different surveying methods, survey timing and local context. We included the natural log-transformation of plot size in all models to most closely resemble species-area relationship theory[92,95]. The covariates of functional group proportions and richness were calculated as the mean values across all years to reflect different values over time in a given plot (**Table S1**). See **Supplementary Results** for an overview of the effects of the sampling design variables on biodiversity metrics. For key results, we additionally fitted univariate models to understand if relationships were consistent without the influence of other covariates (**Table S2**).

We fitted hierarchical models with different data families depending on the structure of the response variable (**Table S1**). These included Gaussian (for numerical values with a normal distribution), negative binomial (for count data where the variance is greater than the mean), beta (for values between 0 – 1, excluding 0 and 1), zero-inflated beta (for values between 0 and 0.99), and zero-one-inflated beta (for values between 0 – 1, including 0 and 1). We specified a prior with a normal distribution for slope and intercept of the negative binomial distribution, and weakly informative priors for the other data families.

When models featured functional group cover or functional group change as covariates, we fitted three models, each including change in one functional group, in order to achieve convergence given that functional group proportions were inherently negatively correlated. These three models included all the same covariates except for the functional group in question and are all represented in the same row under FG and PCHG models in **Table S1**.

We performed ordination analyses to understand whether community homogenisation or heterogenisation had taken place. In order to assess temporal changes in spatial turnover, we calculated spatial dissimilarity in species composition at the first time point for all subsites, and at the last time point separately. Principal Coordinate Analyses (PCoAs) were carried out with the 'vegan'[96] and 'ape'[97] R packages. We calculated multiple β-diversity dissimilarity metrics (Jaccard, Sørensen, Bray-Curtis, Modified Gower, Manhattan and Euclidian) for both the start and end time point of all 73 subsites. These dissimilarity metrics had varying degrees of emphasis on presence-absence versus abundance turnover[98].

Subsequently, we calculated homogeneity of variance between the mean distance to centroid for start and end subsites, following the methodology outlined in Anderson et al. (2006)[99], and assessed the difference in mean distance to centroid between start and end time subsites through ANOVAs. Here, centroids indicate the average community composition across subsites. Then, we calculated the distance between start and end time points per subsite within the PCoA space for two β-diversity metrics (Jaccard and Bray-Curtis) through Cartesian coordinates(1), where x_2 and y_2 refer to the final timepoint per subsite and x_1 and y_1 refer to the start timepoint per subsite. These values reflected the change in community composition and abundance relative to the start time point of each subsite. Next, we modelled the distances between PCoA coordinates as response variables against the set of fixed effects in **Table S1**.

Finally, we calculated the difference in the distance to centroid between start and end time for each subsite, and modelled those values as response variables against the set of fixed effects (**Table S1**). These values reflected the difference in each subsite relative to the overall mean composition of subsites across the tundra. An overall decrease in this distance across all subsites would indicate compositional homogenisation. As these analyses were carried at the subsite level, all variables were imputed as means per subsite considering the values of species abundances in all plots within each subsite.

$$^{(1)}\ Distance\ between\ PCoA\ coordinates = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

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