# Plant diversity dynamics over space and time in a warming Arctic

Mariana García Criado[1]*, Isla H. Myers-Smith[1,2], Anne D. Bjorkman[3,4], Sarah C. Elmendorf[5], Signe Normand[6], Peter Aastrup[7], Rien Aerts[8], Juha M. Alatalo[9], Lander Baeten[10], Robert G. Björk[4,10], Mats P. Björkman[3,11], Noémie Boulanger-Lapointe[12], Ethan E. Butler[13], Elisabeth J. Cooper[14], J. Hans C. Cornelissen[8], Gergana N. Daskalova[15], Belen Fadrique[16], Bruce C. Forbes[17], Greg H. R. Henry[18], Robert D. Hollister[19], Toke Thomas Høye[20], Ida Bomholt Dyrholm Jacobsen[21], Annika K. Jägerbrand[22], Ingibjörg S. Jónsdóttir[23], Elina Kaarlejärvi[24], Olga Khitun[3], Kari Klanderud[25], Tiina H. M. Kolari[26], Simone I. Lang[27], Nicolas Lecomte[28], Jonathan Lenoir[29], Petr Macek[30,31], Julie Messier[32], Anders Michelsen[33], Ulf Molau[3], Robert Muscarella[34], Marie-Louise Nielsen[20], Matteo Petit Bon[27,35], Eric Post[36], Katrine Raundrup[21], Riikka Rinnan[33], Christian Rixen[37], Ingvild Ryde[33], Josep M. Serra-Diaz[38,39], Gabriela Schaepman-Strub[40], Niels M. Schmidt[7], Franziska Schrodt[41], Sofie Sjögersten[42], Manuel J. Steinbauer[43], Lærke Stewart[44], Beate Strandberg[20], Anne Tolvanen[45], Craig E. Tweedie[46] and Mark Vellend[47].

**Author details**

1. School of GeoSciences, University of Edinburgh, Edinburgh, Scotland, UK
2. Department of Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Canada
3. Department of Biology and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden
4. Gothenburg Global Biodiversity Centre, Gothenburg, Sweden
5. Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, CO, USA
6. Department of Biology, Aarhus University, Aarhus, Denmark
7. Department of Ecoscience, Aarhus University, Roskilde, Denmark
8. Amsterdam Institute for Life and Environment (A-LIFE), Amsterdam, The Netherlands
9. Environmental Science Center, Qatar University, Doha, Qatar
10. Forest & Nature Lab, Ghent University, Belgium

11. Department of Earth Sciences, University of Gothenburg, Gothenburg, Sweden
12. Department of Geography, University of Victoria, British Columbia, Canada
13. Department of Forest Resources, University of Minnesota, St. Paul, USA
14. Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, N-9037 Tromsø, Norway.
15. Biodiversity, Ecology and Conservation Group, International Institute for Applied Systems Analysis, Schloßpl. 1, 2361 Laxenburg, Austria
16. School of Geography, University of Leeds, Leeds, LS2 9JT, UK
17. Arctic Centre, University of Lapland, FI-96101 Rovaniemi, Finland
18. Department of Geography, University of British Columbia, Vancouver, BC V6T 1Z2 Canada
19. Biology Department, Grand Valley State University, Allendale, Michigan, USA
20. Department of Ecoscience and Arctic Research Center, Aarhus University, Aarhus, Denmark
21. Greenland Institute of Natural Resources, Nuuk, Greenland
22. Department of Electronics, Mathematics and Natural Sciences, Faculty of Engineering and Sustainable Development, University of Gävle, Gävle, Sweden
23. Life- and Environmental Sciences, University of Iceland, Sturlugata 7, 102 Reykjavík, Iceland
24. Organismal and Evolutionary Biology Research Programme, University of Helsinki, Finland
25. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Aas, Norway
26. Department of Environmental and Biological Sciences, University of Eastern Finland, Yliopistokatu 7, FI-80101 Joensuu, Finland
27. Department of Arctic Biology, University Centre in Svalbard, N-9171 Longyearbyen, Svalbard, Norway
28. Canada Research Chair and Centre d'Études Nordiques, Department of Biology, University of Moncton, Moncton, New Brunswick, Canada
29. UMR CNRS 7058, Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, Amiens, France
30. Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, Na Sadkach 7, 370 05 Ceske Budejovice, Czech Republic

31. Chair of Biodiversity and Nature Tourism, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5a, Tartu 51006, Estonia
32. Department of Biology, University of Waterloo, Waterloo, Canada
33. Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark
34. Plant Ecology and Evolution, Evolutionary Biology Center, Uppsala University, Sweden
35. Department of Wildland Resources | Quinney College of Natural Resources and Ecology Center, Utah State University, UT-84322 Logan, Utah, USA
36. Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 95616 USA
37. WSL Institute for Snow and Avalanche Research SLF, Switzerland
38. Department of Ecology and Evolution, University of Connecticut, CT, USA
39. Université de Lorraine, Agroparistech, INRAE, SILVA, 54000 Nancy, France
40. Dept. of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
41. School of Geography, University of Nottingham, Nottingham, UK
42. University of Nottingham, School of Biosciences, Sutton Bonington Campus, Collage Road, Loughborough, LE12 5RD, UK
43. Bayreuth Center of Sport Science (BaySpo) & Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, 95447 Bayreuth, Germany
44. Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway
45. Natural Resources Institute Finland, Paavo Havaksen tie 3, 90570 Oulu, Finland
46. Department of Biological Sciences University of Texas at El Paso, El Paso, TX 79968
47. Département de biologie, Université de Sherbrooke, Québec, Canada
(*) Corresponding author: mariana.garcia.criado@gmail.com

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MGC conducted the analyses and wrote the manuscript, with contributions from all authors. ITEX+ contributors provided plant composition data, and ArcFunc participants contributed to the initial study framework.

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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[1], and plant communities are responding through shifts in species abundance, composition and distribution[2–4]. However, the direction and magnitude of local plant diversity changes have not been quantified thus far at sites across the Arctic. 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 temporal changes in species richness and composition from repeat surveys conducted over different intervals between 1981 and 2022, and identified the geographic, climatic and biotic drivers behind these changes. We found greater species richness at lower latitudes and warmer sites, but no indication that local species richness was changing directionally over time, on average. However, species turnover was widespread, with 59% of plots gaining and/or losing species. Proportions of species gains and losses were greater where temperatures had warmed most. Shrub expansion, particularly of erect shrubs, was associated with greater species losses and decreasing richness. Despite changes in plant composition, 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 plant communities changed in richness and composition in different directions, with temperature and plant-plant interactions emerging as the main drivers of directional change. Our findings demonstrate how climate and biotic drivers can act in concert to alter plant composition, which could be the precursor of future biodiversity change with impacts on ecosystem function, wildlife habitats and livelihoods for Arctic people[5,6].

# Introduction

Climate change is altering biodiversity patterns on Earth[7,8]. Elevated rates of species extinctions have led to biodiversity loss at the global scale[9,10]. At regional scales, biotic homogenisation has been observed[11,12], while at local scales studies have shown increased turnover, but often no net richness change[13,14]. Climate change impacts on biodiversity have been observed across temperate and tropical biomes[8,15]. However, surprisingly little is known about changes in species diversity at northern latitudes, despite Arctic ecosystems experiencing four times faster warming than the global average[1]. While rapid warming is expected to alter the diversity of Arctic vascular plant communities, the direction of local diversity change remains uncertain[2,16], particularly since local changes in species richness do not necessarily translate into large-scale biodiversity trends[17]. Plants are the foundation of Arctic terrestrial food webs, the carbon cycle and the livelihoods of Arctic people. Thus, in order to understand climate change impacts on Arctic ecosystems, we must first quantify impacts on terrestrial plant communities.

Arctic plant diversity change could be shaped by interacting processes following four pathways. (1) If species migrate northward to track climate warming, we would expect a net increase in overall Arctic plant species richness[2,18,19]. (2) Richness increases could also result from short-distance dispersal and colonisation events from species that are already present in neighbouring local species pools, as growing conditions improve and communities are potentially able to support more species[20,21]. (3) Conversely, reduced Arctic floral diversity could result from losses of cold-adapted species[22] that cannot cope with increasing temperatures[23]. (4) These declines could be exacerbated by increased competition with colonising species originating from Low Arctic and boreal latitudes[24,25] or by local species becoming better competitors under warmer conditions[4]. Because these pathways may be acting in concert, it is possible and indeed likely that richness increases and decreases could occur simultaneously, resulting in no net richness change. Yet, the effects of these different pathways on current and future Arctic plant diversity trends remain poorly understood. We address this knowledge gap by quantifying the direction and magnitude of Arctic vascular plant diversity change over time at the local level (α-diversity) and temporal turnover in species composition (β-diversity), and investigating which geographic, climatic and biotic drivers are related to different aspects of diversity change in order to understand trends across the Arctic.

Apart from evolutionary history and biogeography, species richness patterns at large scales are broadly driven by climatic gradients[26]. Many taxa exhibit a latitudinal gradient in diversity, whereby species richness is greater at lower latitudes, which are generally warmer[27,28]. Thus, Arctic vascular plant richness is expected to increase over time as rapid warming[1,29] leads to new, warmer thermal niches for warm-adapted species at northern latitudes. This expectation is further supported by observed increases in vascular plant species richness with warming across European mountain tops[30,31], whose elevational gradients mirror Arctic latitudinal climatic and richness gradients[32]. 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')[33–35] and because the dissimilarity between Low Arctic and boreal flora is more pronounced than the dissimilarity between High and Low Arctic flora[36]. Overall, we expect richness increases where more warming has occurred, and at lower latitudes closer to the boreal zone.

Warming-driven shifts in biotic interactions are another key driver of changes in species distributions and community composition[3,37]. Changes in dominance of different functional groups (e.g., graminoids, forbs, shrubs) can impact plant diversity and abundance of the entire plant community[5]. For example, shrub expansion has been associated with decreases in lichen, bryophyte and bare ground cover[2,16]. Traits such as higher and denser canopies allow tall shrubs to outcompete shorter species for light via shading[3,38,39], and deciduousness that results in greater litter fall can smother shorter plants[40,41].An increase of nitrogen-fixing tall shrubs (e.g., alder) may also lead to increased soil nitrogen and result in suppression and competitive exclusion of non-nitrogen-fixing vegetation [24,42]. Tundra species with high light and specific nutrient requirements, or specialized in cold environments, may be particularly vulnerable to a changing competitive environment, with rare species at greater risk of local extinction[43], as has been observed in Arctic-alpine ecosystems[22]. Overall, a decline in species richness may be expected where shrub cover has increased over time.

Shifts in species composition due to warming are likely to lead to temporal changes in the spatial dissimilarity (i.e., spatial β-diversity changes over time) of plant communities across the Arctic. Climate change might lead to ecological communities experiencing biotic homogenization, as observed in other biomes such as tropical[44] and temperate forests[12]. Arctic vegetation might become spatially more homogeneous (i.e., lower β-diversity) due to the expansion of dominant and widespread species[45], such as dwarf shrubs across the High Arctic, as a result of reduced winter mortality and increased recruitment with warming[46,47]. At the forest-tundra ecotone, shrub expansion could lead to biotic homogenisation as shrubs become more dominant[48]. However, habitat heterogenization could also occur[45]. For example, permafrost thaw and hydrology changes with warming could lead to the development of novel wetland plant communities[49,50]. Moreover, the borealisation of Arctic ecosystems close to the treeline could further differentiate Low and High Arctic plant communities[51]. In sum, whether Arctic plant communities will become more or less similar to each other with climate change remains uncertain.

Here, we quantify multiple dimensions of local Arctic vascular plant diversity: richness, richness change, evenness (Pielou), evenness change, temporal turnover based on presence-absence and abundance (Jaccard and Bray-Curtis), and species trajectories (proportions of species gains, losses and persistence) over time (**Table S1, S2, S3**). We additionally evaluate changes in subsite-level composition over time using Principal Coordinate Analyses (PCoAs). We used 42,234 records from 2,174 plots in 45 study areas (**Figure 1a**) encompassing 490 vascular plant species (**Figure S1**, **S2**). (1) We quantify spatial patterns in Arctic diversity across latitudinal and climatic gradients, in order to inform our expectations of diversity changes in response to warming. (2) We identify the specific geographic (latitude, biogeographic region), climatic (moisture, warmest quarter temperature, precipitation, and their change over time), biotic (functional group cover and its change over time), and sampling variables (plot size, plot-level species richness and monitoring duration) associated with Arctic diversity change. (3) We investigate whether vascular plant communities across the Arctic are becoming more similar (e.g., declining β-diversity) over time. Our monitoring dataset from the International Tundra Experiment Plus database (ITEX+) consists of marked plots with plant species composition surveyed at different intervals between

1981 and 2022 (**Figure 1d**, **S3**). ITEX+ sites have a hierarchical structure, with species composition data recorded at the plot level. There are multiple plots within a subsite, and often multiple subsites within a study area (**Figure S4**). The 45 long-term monitoring study areas capture most of the variation in temperature and precipitation across the Arctic tundra (**Figure 1b, S5**) and represent diverse assemblages of tundra functional groups (**Figure 1c**, **S6**). We address three main research questions (RQ):

1) How and why has Arctic vascular plant richness changed over time?

We expect an overall increase in plot-level richness (α-diversity) over recent decades across the Arctic[19]. We expect greater richness increases in warmer sites and at lower latitudes, which are closer to boreal forest species pools[33], paralleling the latitudinal biodiversity gradient[52]. Despite the presence of some shade-tolerant species, we also hypothesize that plant species richness will decline overall where shrub cover increases over time, since sun-loving plants could be out-competed by shading and increased litter production from taller and denser shrub canopies, as per spatial analyses[24]. Thus, tundra plant communities close to treeline could follow different trajectories in shrub-dominated versus open tundra plant communities.

2) How and why has temporal plant species turnover changed?

We hypothesise an increase in plot-level turnover and species replacement with warming[42] and increasing shrub cover[2]. We expect proportionally greater species gains with warming as a result of increases in thermophilic species[53]. Where shrubs are increasing in dominance, we expect greater species losses due to shading and litter production[24].

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

Despite uncertainty, we hypothesise biotic homogenisation of plant communities (declining spatial β-diversity through time)[47]. This homogenisation could be caused by an infilling of warmer thermal niches[34,46,47] by the same increasingly dominant species with higher growth rates, good dispersal and colonisation capacities[53], which will outweigh proportional species gains.

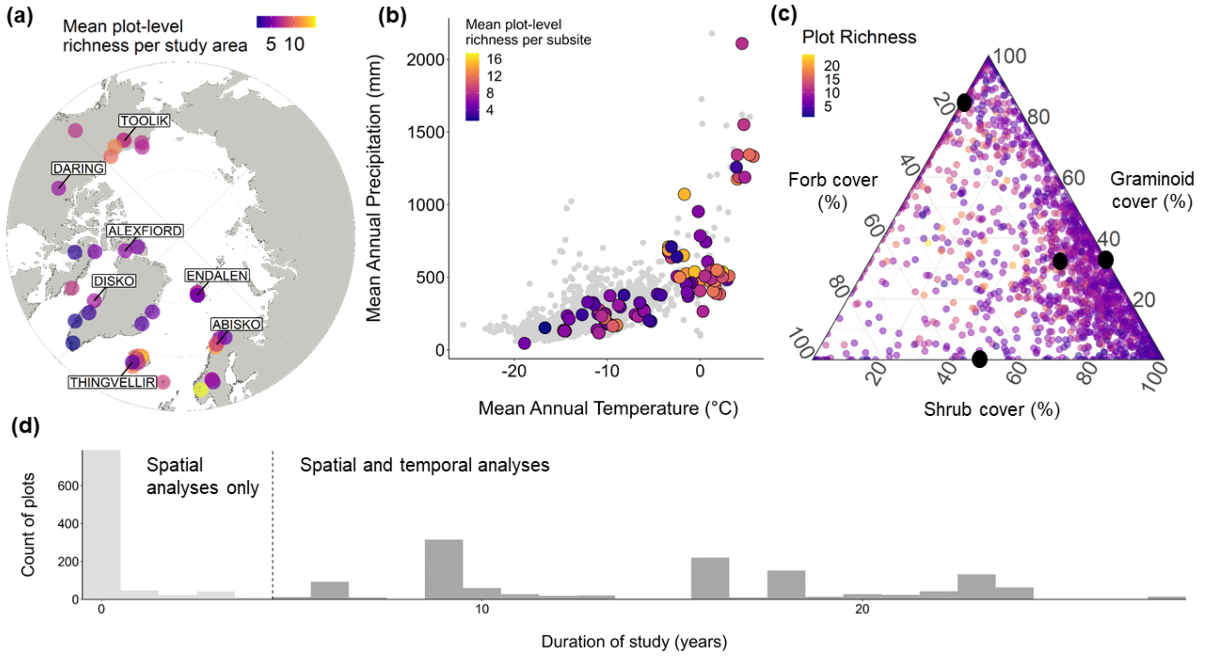

**Figure 1. Representation of our dataset within the geographical, climatic and biotic space, and its temporal resolution. a)** Distribution of study areas, coloured according to mean plot-level vascular plant richness per study area (*n* = 45). This mean calculation is done for visualisation purposes 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°. 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, coloured according to their mean plot-level richness. Background grey points represent a selection of randomly extracted geographic coordinates from the Circumpolar Arctic Vegetation Map[36], including 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 (**Figure S5**). **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. Cover of all three functional groups were negatively correlated, 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. 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. **d)** Duration of monitoring for each plot in our dataset (*n* = 2,174). Only plots that were monitored for over five years (in dark grey) were included in temporal analyses (*n* = 1,266 plots), while those shorter than five years (in light grey) were only included in spatial analyses (*n* = 908 plots). The dashed line indicates the five-year duration boundary. For a survey timeline of all plots, see **Figure S3**.

# Results

## Richness patterns and trends over time

We found support for the extension of the latitudinal species richness gradient across the Arctic (**Figure 1a**), with higher spatial plot-level richness at lower latitudes (slope = -0.03 log(species) degree$^{-1}$, corresponding to a decrease of around one species per every 5° increase at mid-range Arctic latitudes, 97.5% CI = -0.05 to -0.01, conditional $R^2$ = 0.67, marginal $R^2$ = 0.1; **Figure 1a**, **S7**, **Table S3.1**). Richness was also greater at warmer sites, with approximately one species gained on average for every 2°C increase in warmest quarter temperature (slope = 0.06 log(species)/°C, 97.5% CI = 0.03 to 0.1, conditional $R^2$ = 0.63, marginal $R^2$ = 0.16, **Table S3.2**) and in plots with greater forb cover and lower graminoid cover (**Figure 1c**, **Table S2**, **S3.4** - **5**). Despite greater plant richness at lower latitudes and warmer sites, Arctic plant richness did not change directionally over time, on average (slope = 0.0021 log(species) year$^{-1}$, 95% CI = -0.0002 to 0.0043, equating to 0.01 species gain per year, conditional $R^2$ = 0.63, marginal $R^2$ = 0.003; **Figure 2b**, **c**, **Table S1**). Species richness change was not related to latitude (**Figure 2a**, **Table S3.51**), nor to long-term warming trends (**Figure 2d**, **Table S4**). There was no interactive effect between temperature and temperature change on richness change (slope = 0.07, 95% CI = -0.65 to 0.78, conditional $R^2$ = 0.13, marginal $R^2$ = 0.03). Declines in richness occurred with increasing shrub cover, and particularly where erect shrubs, but not dwarf shrubs, increased over time (**Figure 2e**, **Table S3.52**, **S3.52b**). Richness change was not dependent on the baseline (i.e., initial) shrub cover (**Figure S8**, **Table S5**). Richness increased over time with increasing forb cover (**Figure 2f**, **Table S3.53**). The effects of shrub and forb change on richness change remained even when extreme values of change were removed from analyses (**Figure S9**). Overall, plots that were more diverse and/or had more evenly distributed species abundance experienced fewer plot-level species gains and losses as a proportion of total species richness (**Figure S10**). Spatial richness and evenness were correlated (**Table S1**, **Supplementary Results**).

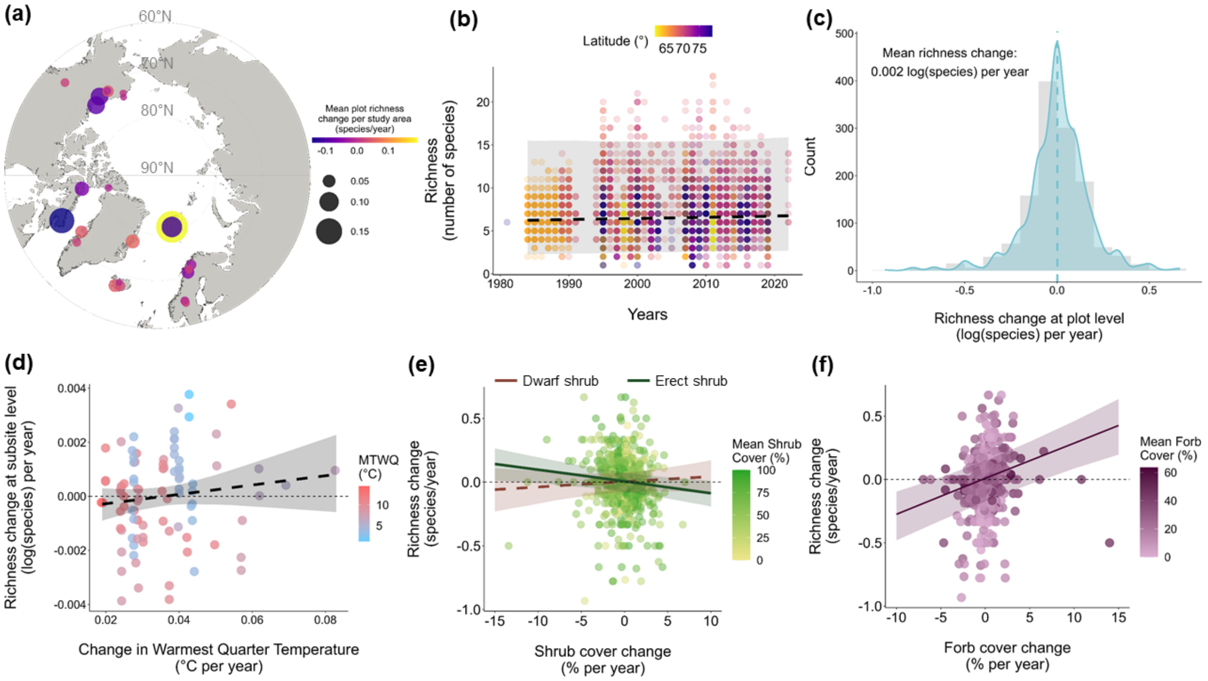

**Figure 2. There was no directional change in species richness across the Arctic on average. a)** There was no clear relationship between species richness change and latitude (**Table S3.51**). Richness change values were calculated as the slope estimate from the linear models of richness change over time per plot (number of species per year), and then averaged at the study area level (*n* = 25) to be represented in the map for visualization purposes only. Points are coloured according to their richness change value as the number of species per year (including positive and negative values) and sized according to their absolute values of richness change. Polar projection with latitudinal bands specified every 10° latitude. **b)** Richness did not change directionally over time. Richness is presented per plot and per year, coloured according to the latitudinal gradient. The dashed line and grey band represent the output from the high-level model in **Table S1**, which includes a nested random effect of plot within year. **c)** Mean richness changes across all plots that were surveyed at least twice over at least five years (*n* = 1,266 plots), calculated as the slope of richness over time per plot. The dashed blue line represents mean richness change. Histogram bin width is 0.1. Model structure and output is from the high-level model in **Table S1**. **d)** Richness did not increase at subsites where long-term warming trends were stronger (warmest quarter temperatures). Points represent richness change computed from slope estimates at the subsite level (*n* = 90), as extracted from the high-level model in **Table S1**, and are coloured according to climatology (long-term temperature means). The dashed line and grey band represent the model estimate and credible intervals. **e)** Richness decreased where erect shrubs (but not dwarf shrubs) increased over time (conditional $R^2$ = 0.16 and marginal $R^2$ = 0.05 for model without shrub categories, and conditional $R^2$ = 0.08 and marginal $R^2$ = 0.007 for model with shrub categories, **Table S3.52, S3.52b**). Richness change estimates (species/year) are extracted from the richness over time linear model per plot. Points are coloured according to mean shrub cover per plot over time. **f)** Richness increased where forbs increased over time (**Table 3.53**, conditional $R^2$ = 0.18 and marginal $R^2$ = 0.07). Richness change estimates (species/year) are extracted from the richness over time linear model per plot. Points are coloured according to forb cover per plot over time. To ensure that the

relationships in **e)** and **f)** were not driven by the most extreme changes in functional group cover, we repeated these analyses by removing the extreme values, which yielded consistent results (**Figure S9**). In all cases, the line indicates the predicted model fit and bands show the 95% credible intervals. Dashed lines indicate an overall model for which the credible intervals on the slope overlapped zero, and solid lines indicate credible intervals that did not overlap zero. All analyses are Bayesian hierarchical models.

## Changes in species composition

Nearly all (99%) of the plots experienced changes in species composition (Bray-Curtis), with 59% of plots either gaining or losing species (Jaccard, **Figure 3a-c**). Arctic communities experienced a mean temporal turnover of 0.22 (Jaccard) and 0.36 (Bray-Curtis) [data bounded between 0 and 1], representing presence-absence (Jaccard) and both presence-absence and abundance-related turnover at the plot level (hereafter, 'abundance-related turnover'). Greater presence-absence temporal turnover (Jaccard) occurred in colder and wetter sites, regions with stronger warming trends, and species-poor plots (**Figure 3a**, **b**, **Table S3.12**, **16** - **18**). Conversely, greater abundance-related temporal turnover (Bray-Curtis) occurred in warmer sites, regions with weaker warming trends (**Figure 3a**, **b**, **Table S3.24** - **26**, **S4**), species-rich plots (**Table S2.19**), and plots monitored over longer periods of time (**Figure S11**). Shrub cover change was not directly related to turnover (**Figure 3c**). Plots experienced substantially more species persisting over time (mean = 5.49 species per plot, 64%) than species gained (1.84, 19%) or lost (1.67, 17%) as a proportion of the plot-level species trajectories (**Figure S12**). Proportions of species gained, persisting and lost were similar across functional groups, and to overall dataset composition (**Figure S13**, $p > 0.05$ for all groups in two-proportion $z$-test, see **Table S6** for top species per trajectory). Species that were more frequently lost across plots were generally rarer (i.e., were found at fewer study areas, slope = -0.13, CI = -0.17 to -0.09, conditional and marginal $R^2 = 0.18$).

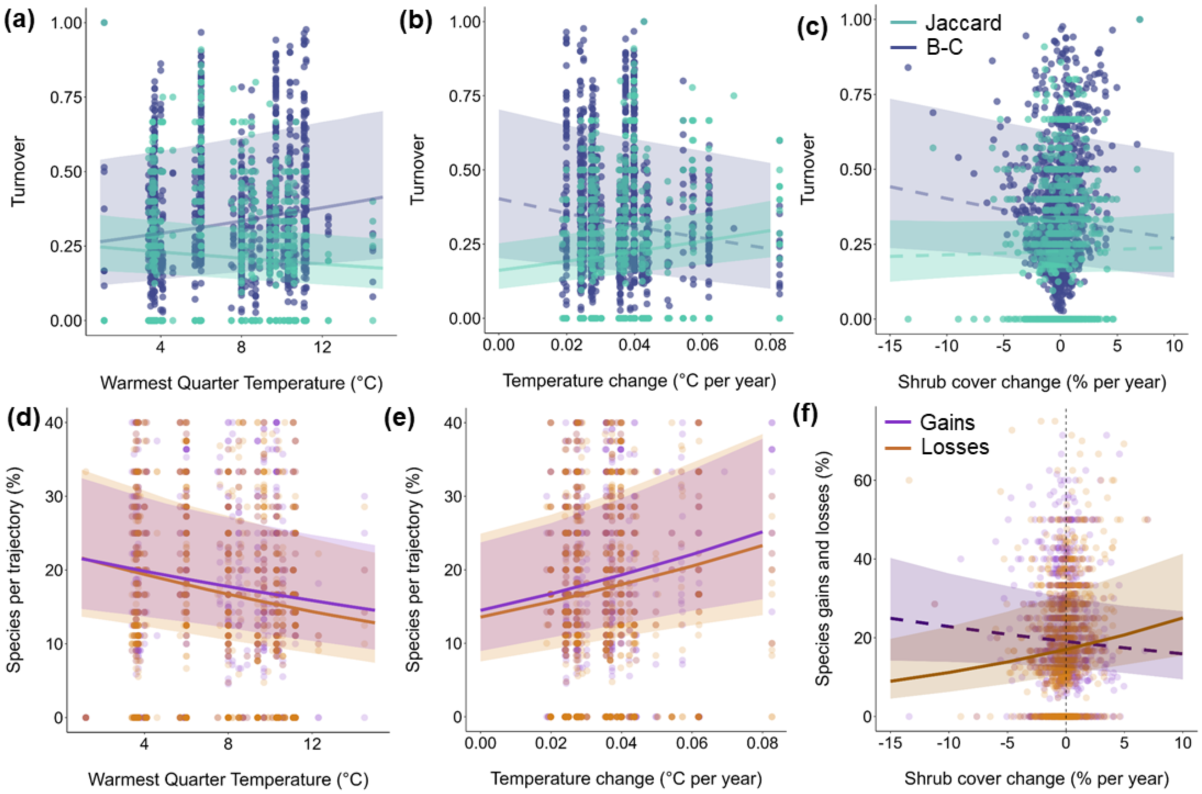

**Figure 3. Local climate, climate change and shrubification influenced species' temporal turnover and trajectories. a)** Relationships between climate (mean temperature of the warmest quarter, MTWQ) and two temporal turnover metrics: Jaccard (presence-absence turnover) and Bray-Curtis (presence-absence and abundance turnover). Model outputs are in **Table S3.12**, **20**, note that the significance of the Bray-Curtis models differed between the univariate and multivariate models (**Table S4**). **b)** Relationships between temperature change over time (slopes from linear models) and the two turnover metrics (*n* =1,266). Model outputs are in **Table S3.16** - **18**, **24** - **26**; note that the significance of the Bray-Curtis models differed between the univariate and multivariate models (**Table S4**). The univariate model is represented here for visualization purposes. Nearly half of the plots (526 plots, 41.5%) did not change at all in terms of presence-absence turnover (Jaccard) and only 6 (0.4%) plots did not change at all when considering both presence-absence and abundance turnover (Bray-Curtis). These plots are indicated by a turnover value of 0 in **a-c**. **c)** Turnover metrics were not directly associated with shrub cover change over time (**Table S3.16**, **21**) **d)** Relationships between MTWQ and the proportion of species lost or gained for each trajectory (persisting species are not displayed). Model outputs are in **Table S3.36**, **44**. **e)** Relationships between MTWQ and the proportion of species lost and gained. Model outputs are in **Table S3.40** - **42**, **48 – 50**. **f)** Increases in shrub cover over time were associated with decreased species gains (though this effect was non-significant), and increased species losses (**Table S2**, **S3.40**, **48**, **S4**). In all cases, lines represent predicted model fits and bands show the 95% credible intervals. Dashed lines indicate that credible intervals on the slope coefficient overlapped zero, and solid lines indicate credible intervals that did not overlap zero. All analyses are Bayesian hierarchical models.

## Species gains and losses were driven by climate and biotic interactions

Species persistence was positively related to mean summer temperature, with colder sites experiencing proportionally more gains and losses than warmer sites (**Figure 3d**, **Table S3.28**, **36**, **44**). Stronger warming trends were associated with lower proportions of plot-level species persistence trajectories and higher proportions of plot-level losses and gains over time (**Figure 3e**, **Table S3.32 - 34**, **40 - 42**, **48 - 50**). There were proportionally more species losses where shrubs had increased (**Figure 3f**; this relationship also held up when removing the most extreme values of change) and graminoids had decreased, and proportionally more species gained where forbs had increased (**Table S2**, **S2.40 - 42**). There were proportionally fewer species gains where shrubs had increased, but the effect was non-significant (**Figure 3f**, **Table S3.45**). See **Supplementary Results** for the effects of geographic and sampling design variables, additional turnover and evenness results, overall functional group composition, and climate change context.

Both warming (**Figure 3b**, **3e**) and shrubification (**Figure 2e**, **3f**) emerged as two main drivers of Arctic plant diversity change. We therefore conducted additional analyses to better understand how and where these drivers interact (**Table S7**). Overall, shrub cover did not increase significantly over time in our dataset (**Table S8**, **S9**). Shrub cover change was not associated with latitude (**Figure S14a**), and the rate of long-term warming was not related to the rate of shrub cover change over time (**Figure S14c**). However, interannual variation in shrub cover was sensitive to temperature, indicating that dwarf shrubs respond negatively while erect shrubs respond positively to warmer temperatures (**Figure S14b**).

## No indication of Arctic biotic homogenisation

Our ordination analyses did not indicate any signs of Arctic-wide biotic homogenisation or differentiation (**Figure 4**). 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 4a**, **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 ± 0.03, end: 0.66 ± 0.03) and Bray-Curtis (start: 0.65 ± 0.04, end: 0.64 ± 0.04) (**Figure 4c**, **d**, **Figure S15**; $p > 0.05$ in ANOVA for all β-diversity metrics). Mean shifts in distance between timepoints per subsite (as Cartesian coordinates, reflecting change in community composition relative to starting point) was 0.035 ± 0.03 (Jaccard) and 0.04 ± 0.03 (Bray-Curtis, **Figure 4e**).

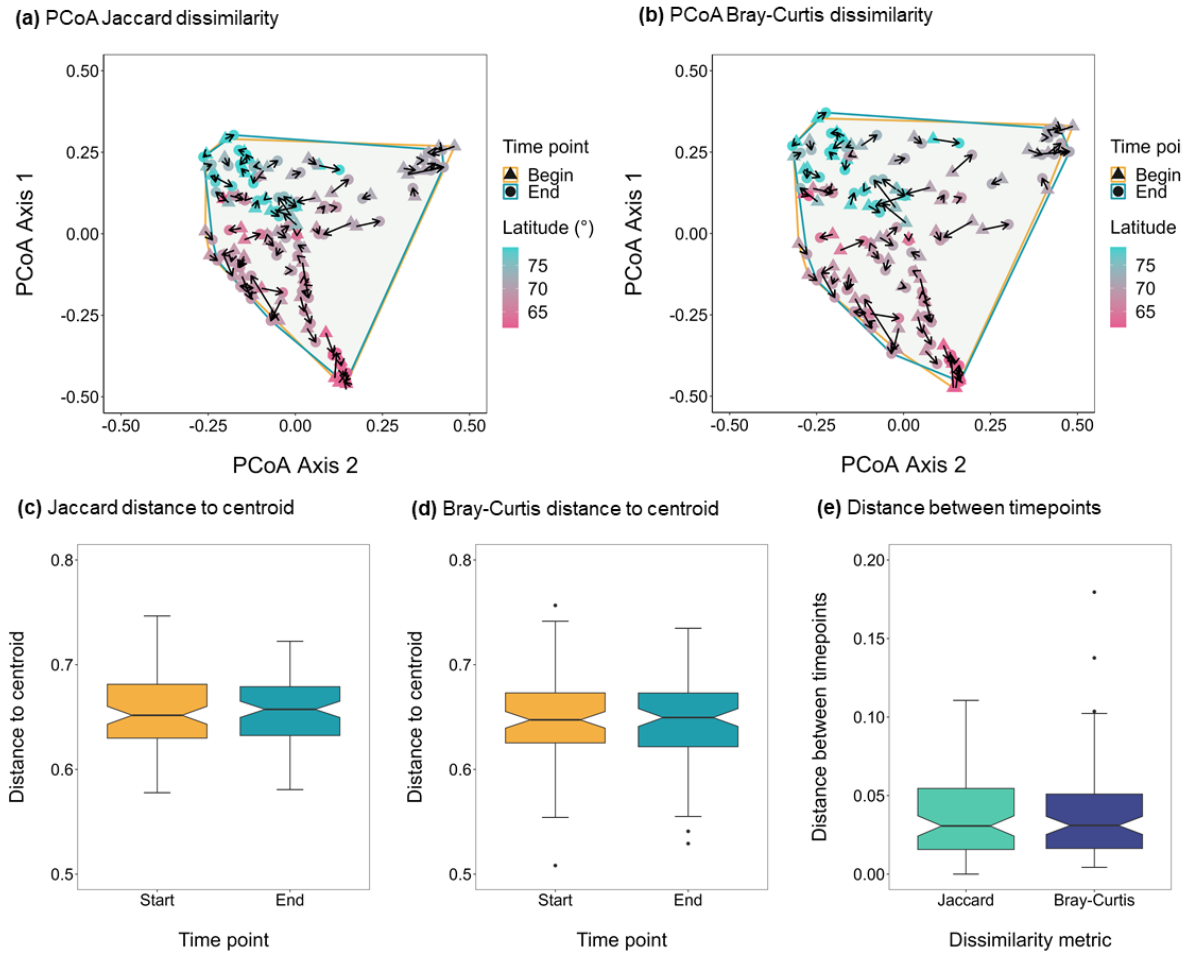

**Figure 4. Subsites showed no homogenisation or differentiation over time across the Arctic.** We calculated temporal change in spatial turnover (β-diversity) between the start (i.e., baseline) and end (i.e., final) time period for all subsites. Principal Coordinate Analyses (PCoAs) are shown with the **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 an arrow per subsite indicating the direction of change over time. Points are coloured according to latitude. Enclosing convex hulls are drawn around subsites. 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. Additional β-diversity metrics are presented in **Figure S15**.

# Discussion

Contrary to our hypotheses, there was no directional trend in plant richness change to date on average (α-diversity; **Figure 2b, c**), despite the Arctic experiencing the greatest rates of warming on Earth over the past decades[1] (**Figure S5b**). This result ran counter to literature predictions[19], experimental observations of plant diversity declines at the local scale[54] and modelling studies predicting a regional declines of 15 to 47% in Arctic-alpine plant species richness[22]. We found that Arctic plant composition and richness change are decoupled, with no net richness change on average despite widespread composition change over time (**Figure 2**, **3**). Consistent with our hypotheses, where diversity changes do occur, they are mainly driven by the combined effects of warming and plant-plant competition, including erect shrub increases[2,24]. Despite the lack of a strong relationship between warming and richness change, both proportional species gains and losses were greater where temperatures increased the most (**Figure 2**, **3**). We found a more consistent influence of shrub increases over time, with relatively greater species losses, thus leading to decreased species richness where shrub cover (particularly of erect shrubs) increased the most over time (**Figure 2**, **3**). We did not find evidence of homogenisation of Arctic vascular plant communities over time, with no directional temporal changes in spatial dissimilarity of species composition (**Figure 4, S15**), indicating that plant communities changed in their composition in a variety of ways. Overall, we found that despite Arctic plant community composition changing to different assemblies based on local context, both climate warming and shrubification emerged as key factors influencing the magnitude of species turnover.

### Mixed influences of climate and climate change on diversity change

Despite spatial species richness being greater at lower latitudes and warmer sites (**Figure S7**, **Table S2**), and rapid Arctic warming over time (**Figure S5b**), species richness did not change directionally (**Figure 2b**). Richness change was not greater towards southern Arctic edges (**Figure 2a**), where we hypothesised that northward migration from the boreal forest (i.e., borealisation) might be a major driver of change. Instead, this lack of latitudinal change might indicate that, where diversity is changing, one of the main sources is colonisations by species present in local species pools that have not yet been recorded in long-term monitoring plots (referred to as 'landscape' or 'dark' diversity)[20,55]. Species richness increases were not greater at sites with greater rates of warming over time (**Figure 2d**), but warming was associated with proportionally greater species gains and losses (**Figure 3e**). While gains could represent warm-adapted species expanding into warmer areas, these could outcompete cold-adapted species[53,56], with biotic interactions usually being more relevant at species' warm edges[57]. This could be generating species losses, together with cold-adapted species being unable to cope physiologically with warming. This suggests that plant community composition is being influenced by warming (**Figure 3b**), but that species gains and losses within plant communities, on average, balance each other (**Figure 3e**, **S12**), consistent with some predictions of equilibrium theory[58] and thus resulting in the observed overall non-directional richness change (**Figure 2b**). With 99% of plots experiencing composition changes via altered relative species abundance (Bray-Curtis > 0), and 66% of plots gaining and/or losing species (Jaccard > 0), composition change could begin to influence richness change over time. Overall, these compositional changes could result in further species reshuffling, losses of rare and ecologically important species, and associated changes to ecosystem function.

### Shrubification as a driver of species richness and composition change

We found that shrubification was associated with richness and compositional change. Increases in shrub cover over time were accompanied by decreases in richness and evenness, and greater proportional species losses relative to sites with decreasing shrub cover (**Figure 2e**, **3f**, **Table S2**). Shrub expansion has been widely reported[2,4,59], though we found only a marginal increase (i.e., the credible intervals overlapped zero) in Arctic shrub cover at the plot scale within the ITEX+ dataset (**Table S9**). Shrub cover change has been widely linked to warming in previous site-level studies[2–4]. However, we did not find clear evidence for greater shrub change with greater rates of warming within this dataset (**Figure S14c**), in agreement with previous pan-Arctic studies[4]. Instead, we found that shrub cover was sensitive to temperature, with erect shrub cover increasing and dwarf shrub cover decreasing with warmer temperatures (**Figure S14b**).

Across space, lower species richness has been observed with greater shrub cover, with shading and litter production leading to decreases in sun-loving plants under shrub canopies[24,25]. Using space-for-time approaches, studies have assumed a similar pattern to occur over time, without necessarily testing it. Here, we found and confirmed this pattern over time: where shrub cover increased over time, community evenness decreased and greater species losses occurred, leading to reduced species richness (**Figure 2e, 3f, Table S1**). 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 rare and/or less competitive species[42,60,61]. Thus, Arctic diversity might be more at risk at sites with increasing shrub cover, particularly from erect shrubs (**Figure 2e**). Conversely, both increasing graminoid and forb cover were associated with increased richness over time, and increasing graminoid cover was related to lower species losses (**Figure 2f**, **Table S2**). Graminoids were more likely to persist than forbs (**Table S2**), 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, greater height and better resistance against herbivory[62–64]. Overall, our findings suggest that species may be more at risk where taller shrubs are expected to increase  due to aboveground competition for light[64,65].

## Plant diversity changed in multiple directions among rapid warming

Our findings demonstrate that Arctic plant richness changed in different directions (**Figure 2b**, **c**) among continued warming. We found that, on average, plots had a majority of species persisting over time (64%, **Figure S12**). Plots with high species richness and more even communities showed the least amount of change, with a lower proportion of species losses and gains (**Figure S10**). This pattern could be a statistical artefact due to smaller species pool sizes leading to proportionally greater gains and losses, or be a result of greater community resistance, due the reduced extinction risk derived from greater richness and lack of species dominance[43,66], as per the diversity-stability relationship[67]. We found that persistence was more common in locally warm and dry environments relative to colder and wetter environments, while there were proportionally more species losses in cold sites relative to warm sites (**Figure 3c**). Homogenisation has been predicted for High Arctic vegetation[46,47], but we found no evidence of either biotic homogenisation nor differentiation (calculated as temporal changes in spatial dissimilarity) in Arctic plant communities thus far (**Figure 4**), in common with global syntheses[45], with no particular directionality of subsite-level change (**Figure 4**). Our findings support the observed global decoupling of compositional and richness change[13,14], as we observed more temporal turnover than directional Arctic richness change. One consequence of temporal turnover is the increase in tundra plant community height over time due to the immigration of taller species[65]. Continued compositional change is likely to lead to additional shifts in plant traits and the functioning of Arctic ecosystems[5,65].

A better understanding of the underlying mechanisms that drive local biodiversity change will be key to identifying future rates and hotspots of change under accelerating warming[20,68]. Further research is required to determine whether Arctic plant communities are  exhibiting resistance to warming[69], as additional processes could contribute to a lack of detected richness change on average. For example, the same species could be both lost and gained across plots over time due to stochastic dynamics or sampling effects (**Table S6**). Future change in species richness and composition may not yet be detected due to extinction lags[70] and slow colonisation rates in communities of long-lived perennial species. Additionally, priority effects could cause heterogeneity in species responses to warming[71]. Variation in topography, microclimate and nutrient availability could mediate ecological responses and buffer against climate change impacts by providing microhabitats with suitable conditions[21,72–74]. Rising temperatures are projected to be accompanied by increasing precipitation leading to a warmer and wetter Arctic, which could ameliorate warming-derived drought effects on plants[50]. In addition, herbivory may mitigate warming-driven shrub expansion in certain regions[54]. Thus, the integration of extinction lags, priority effects, local context, and both micro- and macroclimate is an essential next step to better identify the mechanisms behind Arctic plant dynamics.

It was not possible to include non-vascular plants (bryophytes and lichens) in our analyses due to inconsistent recording across plots[75], but their influence on vascular plant dynamics cannot be discounted. Bryophytes can suppress vascular plant regeneration[76], while both lichens and mosses have a strong buffering effect on microclimate extremes, and can thus mitigate further shrubification[77]. 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. Further, the presence or absence of certain bryophytes reflect subtle differences in changing surface hydrology (e.g., drying, paludification), soil chemistry, and disturbance[78,79], which can in turn affect species composition. A future priority will be to expand non-vascular plant surveys to obtain a comprehensive view of plant biodiversity change and biotic interactions among functional groups.

Overall, we found that changes in Arctic plant diversity and community composition depend on local context, with both warming and shrubification emerging as key factors influencing the magnitude of species turnover. Probable mechanisms underlying the observed diversity changes include colonisations from local species pools[20], gains of thermophilous species[53], losses of less competitive and/or rare species[56] and increased competition with canopy-forming shrubs[24]. Our results indicate that we should not expect an overall loss or gain of vascular plant biodiversity with warming in the Arctic. Instead, directional change in plant communities will depend on the combination of changing environmental conditions and available species pools, with warming leading to greater plant community composition change and shrubification resulting in decreasing species richness over time. This research demonstrates the value of long-term *in situ* monitoring at local scales for the detection of biodiversity change and improving our understanding of biome-wide responses or resistance to climate warming[80]. The extensive reshuffling of Arctic vascular plant composition in recent decades observed in this study underscores the urgent need to explore the impacts of these shifts on ecosystem function, wildlife habitats, and livelihoods for Arctic peoples[5,6].

# Methods

## Plant composition data

We extracted composition and abundance data from the International Tundra Experiment (ITEX+) dataset[80,81]. 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. We only kept control (ambient) plots and not experimental data. All ITEX+ sites have a hierarchical structure, with species abundance and composition data recorded at the plot level, 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. We refer to these terms throughout to indicate specific levels of this hierarchy, and we use the terms ‘plant communities’ or ‘sites’ when referring more generally to groups of Arctic species at any scale or resolution. Our analyses were carried with plot as the replication unit, unless specified otherwise.

Our dataset contained 2,174 plots, and they were all retained for spatial analyses. For temporal analyses, we retained the 1,266 plots (58.2%) that had been surveyed at least twice over a minimum of five years, since shorter timeseries tend to overrepresent real change in Arctic communities[17,65]. The remaining 908 plots (41.7%) were only used in the spatial analyses (**Figure 1d**, **S3**). 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 (**Figure S3**).

Plots range in size (i.e., surveyed area) based on the plant species community of interest and landscape characteristics[80,82] (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 three subsites per study area (range = 1 to 11). The total surveyed area per subsite (calculated as plot size * number of plots per subsite) is generally constrained under 20 m$^2$ (**Figure S4**). Plots were monitored over different periods during four decades (**Figure 1d**, **S3**), with a mean study duration of eight years (range = 1 to 28), a mean of three monitoring time points per plot (range = 1 to 11) and a mean time between surveys of five years (range = 1 to 26).

For data cleaning (taxonomic verification, input errors), we followed the same protocol as Bjorkman et al. (2018)[65]. Additionally, we retained only Arctic and sub-Arctic 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[83–

[85]. We kept only plots whose surveyed area was ≤ 1 $m^2$ in order to ensure comparable richness values across plots, given that plant species richness tends to increase with plot size[86]. Since Arctic plants are relatively small individuals, a plot size of 1$m^2$ is appropriate to reflect ecological assembly processes at the local scale[87]. We included the natural log-transformation of plot size in all models (except for evenness) to account for variability among plot sizes to most closely resemble species-area relationship theory[86,88]. We did not include the plot size term as a fixed effect in evenness models as the evidence of a relationship between plot size and evenness is mixed, with studies finding positive, negative and no relationships[89], and thus there are no clear theoretical reasons to expect such a relationship. We tested an additional plot size sensitivity analysis by re-running models behind some of the main manuscript outcomes (**Table S2.45** and **S2.52**) but only with plots whose size was 1$m^2$ ($n$ = 631 and 597 for the main analysis and the sensitivity analysis, respectively). Both estimates of temperature change and shrub cover change had the same direction and significance as their original model counterparts.

Since plots were surveyed by different methods, we included only plots which were surveyed using % cover as an abundance metric and/or another metric that was convertible to percentage cover, including point-framing and cover-class methods (e.g., Braun-Blanquet). We kept all types of point-framing data (top hit, top-bottom hits and all hits) since values of overall richness were similar across methods (**Figure S1**). 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 S1**). We converted all values to relative cover (0 - 100%) to ensure consistency across survey methods (**Figure S2**). 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 and forbs), so that the total vascular plant cover was 100% in each plot-by-year. We also calculated the proportion of functional group cover 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 ‘lower’ 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 models (as shrub % change, graminoid % change and forb % change, **Table S2**). 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. When models featured functional group cover or functional group change as covariates (FG or PCHG models, see 'Model types' below and **Table S2**), 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 S2**.

## Climate data

We extracted, at the subsite level, data from long-term climatologies at CHELSA (version 1.2.1)[90] including mean annual temperature, mean temperature of the warmest quarter (MTWQ) per year, mean temperature of the coldest quarter (MTCQ) per year and mean annual precipitation (MAP, hereafter 'precipitation') for the period 1979 - 2013. Upon examining correlations between the three temperature variables, we found that most were correlated with each other. Thus, for our temperature variable we used MTWQ (hereafter 'temperature') as it best represents the growing season conditions and has been previously linked to plant biomass, growth and reproductive rates[91–93], which are in turn relevant variables driving diversity change. Additionally, we extracted time series of the daily mean air MTWQ per year and annual precipitation amount during the period 1979 to 2013.

We calculated change over time in temperature and precipitation by fitting linear models of yearly climatic values over this time period, and used the slopes of change per plot as fixed effects in the multivariate models described below (as temperatureand precipitation change, **Table S2**). Since geographic coordinates are only available at the subsite level, 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 (**Table S2**). We chose CHELSA as the source for our climate data because, as a quasi-mechanistical statistical downscaling product, it has a very fine grain size

(1x1 km) and has been shown to outperform other interpolation-based climate products, and particularly for precipitation[90,94,95].

## Biodiversity metrics

We chose to analyse common biodiversity metrics that capture species diversity, dominance, and composition change, rather than composite indices, in order to examine the specific elements of biodiversity in isolation from each other. Richness was defined as the total number of species co-occurring in a plot. We acknowledge that some authors refer to this term as 'species density' when it is based on an area metric[96], but hereafter we refer to 'richness' as a more common term in the literature. 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[88].

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 originally calculated as counts, and then transformed to proportions in order to account for the inherent variability in species richness across plots. Species proportions were calculated by dividing the number of species per trajectory in a plot by the total number of species in each plot at both time points combined (i.e., total number of unique species present at each plot in both timepoints, including losses, gains and persisting species). This approach allows for an overview of species trajectories per plot, and also for comparability across plots.

## Statistical analyses

We employed a Bayesian framework for all analyses. We used the software and programming language R version 4.1.0[97]. Models were fitted using the 'brms' package[98] and ran for as many iterations as necessary to achieve convergence (2,000 to 3,000 iterations over four chains), which was assessed through examination of the $R_{hat}$ term and trace plots.

## Data families

We fitted hierarchical models with different family distributions depending on the structure of the response variable (**Table S1, S2**). These included Gaussian family with an identity link function (for continuous response variables with a normal distribution), negative binomial family with a log link function (for count data where the variance is greater than the mean), beta family with a logit link function (for values ranging between 0 and 1, but excluding 0 and 1), zero-inflated beta family with a logit link function (for values ranging between 0 and 0.99), and zero-one-inflated beta family with a logit link function (for values between 0 and 1, including 0 and 1). For the beta family, we included in our models 'zi ~ 1' (where zi is the probability of being a zero), 'zoi ~ 1' (where zoi is the probability of being a zero or a one), and 'coi ~ 1' (where coi is the conditional probability of being a one, given that an observation is a zero or a one). In the case of the spatial richness models (**Table S2.1-5**), the log link function with a negative binomial distribution assumes the relationship between richness and plot size to be log-log: log(richness) ~ log(plot size). We specified weakly informative priors for beta and negative binomial families. Data families for each model are specified in **Table S1, S2.**

## High-level models

To obtain the mean richness and evenness change estimate across the tundra, we fitted hierarchical models of richness and evenness per year over time and included nested random slopes per plot within the subsite (**Table S1**). In these two models, the year covariate was centred as needed to achieve model convergence. From the richness change over time model, plot-level estimates were extracted to visualize overall richness change over time (**Figure 2b, c**) and subsite-level estimates were extracted to fit the richness change ~ temperature change model (**Figure 2d**, **Table S4**).

## Multivariate models

We fitted three main types of multivariate models: spatial, two time-point and temporal (**Table S2**). 1) Spatial models refer to current diversity metrics across space, with one unique value of the response variable (richness, evenness) measured at the last surveying timepoint. These models identify the main drivers behind spatial patterns of plant diversity. 2) Two-time point models consider 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, and proportions of species losses, gains and persisting species). 3) Temporal models reflect metrics whose response variable had multiple values over time, and at a minimum two timepoints over five years (richness change, evenness change, models derived from the spatial homogenisation over time analyses). For these temporal models (richness change and evenness change), we followed a two-step modelling approach to examine diversity 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); these are referred to as 'change over time models' (CHG). 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 (SUBS in **Table S2**). Both two-time point models and temporal models identify the main drivers behind temporal patterns of plant diversity change (cf. RQ 1, 2).

Across all three model types (spatial, two-time point and temporal) and for each response variable, we fitted several multivariate models (i.e., geographical (GEO), climatic (CLIM), functional group composition (FG), change over time model (CHG), plot change over time (PCHG), subsite (SUBS)) depending on the scale at which the covariates affected the response variable, in order to avoid collinearity and obscuring patterns between fixed effects (**Table S2**, **S3**). 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 key results, we additionally fitted univariate models to understand if relationships were consistent with the multivariate model results without the influence of other covariates (**Table S4**).

## Sampling design covariates

All multivariate models (**Table S2**) included a set of relevant sampling design variables to account for different surveying methods ('plot size'), survey timing ('duration') and local context ('mean richness'). We included the natural log-transformation of plot size in all models to account for variability among plot sizes and for the fact that different plot sizes may lead to different chances to detect changes over time[17,88]. Mean richness was calculated as the mean values of richness across all years to reflect the most common conditions in a plot over time (**Table S2**). Duration was calculated as the difference between the last and the first years of surveying per plot. See **Supplementary Results** for an overview of the effects of the sampling design variables on biodiversity metrics.

## *Post hoc* analyses

In order to understand the relationship between two of the main drivers of diversity change, shrub cover change and warming over time, we performed extra analyses (**Figure S14**, **Table S7**), given that previous literature suggests a positive relationship between them[4,99]. First, we modelled shrub increases as a function of latitude, with a subsite random effect (**Figure S14a**). To identify whether shrubs exhibited sensitivity to temperature, we calculated the mean temperature of the past five years for each monitoring time point (**Figure S14b**). We centred temperatures per subsite prior to analyses in order to standardise magnitudes across regions and to enable model convergence. We modelled shrub cover at each time point as a function of mean temperature of the past five years, with a nested random effect structure of plot within subsite, and an interaction term of shrub type (dwarf versus erect). Additionally, we modelled shrub cover change per plot as a function of long-term temperature change (over the 1978 to 2013 period), with a random effect of subsite and an interactive term of shrub type (**Figure S14c**). To assign shrub categories, we followed the methodology from García Criado et al.[100] and categorised shrubs as dwarf and erect (including low and tall shrubs), since we were interested in the ecological effects of species sprawling versus erect physiognomy.

## Additional models

A number of models were fit outside the context of the already described high-level models, multivariate models and *post hoc* analyses described above. 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 S5**). To understand whether species losses were related to rarity, we modelled the proportional losses per species (as percent of losses relative to all trajectories across plots) as a function of the number of study areas where the species was present in our dataset. To understand whether our temporal turnover versus richness models reflected *a priori* relationships or whether there was a meaningful biological relationship, we compared them with null models. To fit null models, we randomly removed 20% species per plot (to simulate species losses), and randomly included 20% species (to simulate species gains). We used this simulated dataset to calculate turnover values (Jaccard and Bray-Curtis). We fitted intercept-only null models with each metric, and modelled Jaccard and Bray-Curtis turnover as a function of species richness.

Snow is another important driver of tundra plant composition. However, analyses of satellite remote sensing products providing snow cover variables[101] showed that gridded layers of snow-related variables contained too many spatial and temporal gaps to generate a reliable time series of snow-cover duration at our sites. Instead, we extracted data on temporal trends, over the period 1950-2021, for three snow-related variables: snow season length, onset of snow season and end of snow season. These three variables were downloaded from the ‘Bioclimatic atlas of the terrestrial Arctic’ database (ARCLIM)[102], at a spatial resolution of ~9 km by 9 km. We fitted a selection of mixed-effects models to analyse temporal changes for a series of biodiversity variables (richness change, Jaccard turnover, Bray-Curtis turnover, persisters, gains, losses, evenness change) with these three snow-related variables as fixed effects, together with sampling design variables (plot size, duration, mean richness). None of the snow variables were significant in either of these models. This might be due to a non-significant ecological effect of snow season length on diversity trends, or instead the result of a scale mismatch. The spatial resolution at which diversity metrics were calculated is 1m$^2$ or smaller, while the spatial resolution at which snow data are available is 9 km. Thus, this scale mismatch precludes us from making any ecological inferences on the effect of temporal trends in snow season length on plant diversity change.

**Ordination analyses**

We performed ordination analyses to understand whether community homogenisation or differentiation had taken place at the subsite level (cf. RQ 3). 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. To aggregate plot-level data into subsite-level data, we calculated the mean cover per species across all plots in a subsite, both for the start timepoint and for the end timepoint. Principal Coordinate Analyses (PCoAs) were carried out with the 'vegan'[103] and 'ape'[104] 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 90 subsites (**Figure S15**). These dissimilarity metrics had varying degrees of emphasis on presence-absence versus abundance turnover[105].

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)[106], 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 S2**.

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 S2**). These values reflected the difference in each subsite relative to the overall mean composition of subsites across the Arctic. An overall decrease in this distance across all subsites would indicate compositional homogenisation.

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

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