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

Author contributions: MGC conceived the study together with ADB (who initiated the study), IHM-S, SCE, and SN. IHM-S obtained funding for the data synthesis research. MGC, ADB and SCE prepared and cleaned the plant composition data from ITEX+.

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.

Acknowledgments: We thank Tora Finderup Nielsen for sharing the starting code for the homogenisation analysis, Jeffrey Kerby for extracting the random selection of Arctic locations, and Claudia Colesie and Vigdis Vandvik for their comments on the first version of the manuscript. We are grateful to those who contributed to the preparation of the ITEX+ database, including Zoe Panchen, Antoine Becker-Scarpitta, Janet Prevéy, Jonathan Von Oppen, Karin Johansson, Jonathan J. Henn and Joseph Everest. We thank all local and Indigenous communities for the opportunity to work with data collected on their lands. MGC was funded by the BritishSpanish Society Award, and MGC, IHM-S and BCF were funded by the EU Horizon 2020 Research and Innovations Programme through the CHARTER project (Grant #869471). IHM-S was funded by the NERC Tundra Time project (NE/W006448/1). ADB was funded by the Knut and Alice Wallenberg Foundation (WAF KAW 2019.0202), the Swedish Foundation for Strategic Research (FFL21-0194), and the Swedish Research Council (2019-05264). SN and ADB were supported by The Danish Council for Independent Research: Natural Sciences (DFF 4181-00565 to SN). SCE and RDH acknowledge funding from NSF-OPP 1836839. EEB was funded by Biological Integration Institutes Grant NSF-DBI-2021898. MPB (27,35) was supported by the Governor of Svalbard (Svalbard Environmental Protection Fund, grant project number 15/128), the Research Council of Norway (Arctic Field Grant, project number 269957), and the National Science Foundation (grant ANS-2113641). MPB (3,11) was funded by the Research and development projects to future research leaders at FORMAS – Swedish Research Council for Sustainable Development grant agreement 2016-01187, and the Latnjajaure Field Station monitoring program by the strategic research environment BECC - Biodiversity and Ecosystem services in a Changing Climate. EP was funded by the US National Science Foundation and the National Geographic Society. NL was funded by the Canada Research Chair Program and the Natural Sciences and Engineering Council of Canada. EK was funded by the Academy of Finland. GND was funded by a Schmidt Science Fellowship. RR was supported by Danish National Research Foundation (DNRF100 and DNRF168). GHRH was funded by the Natural Science and Engineering Council of Canada, ArcticNet and the Canadian International

Polar Year Program, with logistical support from Polar Continental Shelf Program and the Royal Canadian Mounted Police. PM was funded by Estonian Academy of Sciences (research professorship for Arctic studies).

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 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 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. However, species turnover was ubiquitous, with 59% of plots gaining and/or losing species. Species gains and losses were greater where temperatures had warmed most. Shrub expansion, particularly of taller 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 with 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 colonization from species that are already present in local species pools[20]. 3) Conversely, reduced Arctic floral diversity could result from losses of cold-adapted species[21] that cannot cope with warming temperatures[22]. 4) These declines could be exacerbated by increased competition with colonising species originating from Low Arctic and boreal latitudes[23,24]. Because these pathways may be acting in concert, it is possible 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 investigating which geographic, climatic and biotic drivers are related to different aspects of diversity change in order to understand trends at the pan-Arctic scale.

Species richness patterns at large scales are broadly driven by climatic gradients[25]. Many taxa exhibit a latitudinal gradient in diversity, whereby species richness is greater at lower latitudes, which are generally warmer[26,27]. Thus, Arctic vascular plant richness is expected to increase over time as rapid warming[1,28] leads to new, warmer thermal niches for warm-adapted species at northern latitudes. This expectation is further supported by observed climate-induced increases in vascular plant species richness across European mountain tops[29,30], whose elevational gradients mirror Arctic latitudinal climatic and richness gradients[31]. 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')[32–34] and because the dissimilarity between Low Arctic and boreal flora is more pronounced than the dissimilarity between High and Low Arctic flora[35]. Overall, we expect richness increases where more warming has occurred, and at lower latitudes closer to the boreal zone.

Biotic interactions are another key driver of changes in species distributions and community composition[36]. 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 plant diversity and abundance[5]. Climate change can also promote shifts in the relative abundance of different functional groups[3]. For example, competition derived from 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[3,37,38], and deciduousness is associated with rapid resource acquisition and litter fall onto shorter plants[39,40]. Thus, the presence and abundance of non-shrub vegetation might decrease due to the shading or nitrogen depletion effect of taller shrubs[23,41]. Since the dominance of generalist and competitive species entails increased local extinction risk for rare species[42], we might expect species richness to decrease where shrub cover has increased over time.

Warming-driven shifts in species composition 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. As observed across other biomes[43], Arctic vegetation might become spatially more homogeneous (i.e., lower β-diversity) due to the expansion of dominant and widespread species[44], such as dwarf shrubs across the

High Arctic, as a result of reduced winter mortality and increased recruitment with warming[45,46]. Similarly, shrub expansion at the forest-tundra ecotone could lead to biotic homogenisation as shrubs become more dominant[47]. In contrast, Arctic landscapes could also become more spatially heterogeneous due to permafrost thaw and hydrology changes with warming, including the development of novel wetland plant communities[48,49]. Furthermore, the borealisation of Arctic ecosystems close to the treeline could further differentiate Low and High Arctic plant communities[50]. 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 (species gains, losses and persistence) over time (**Table S1**). 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 composition 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. We expect greater richness increases in warmer sites and at lower latitudes, which are closer to boreal forest species pools, paralleling the latitudinal biodiversity gradient[51]. We hypothesize that plant richness will decline 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[23].

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

We hypothesise an increase in plot-level turnover and species replacement with warming and increasing shrub cover. We expect greater species gains with warming as a result of increases in thermophilic species[52] and greater species losses with increasing shrub cover due to shading and litter production[23] .

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

We hypothesise biotic homogenisation of plant communities (declining spatial β-diversity through time)[46]. This homogenisation could be caused by an infilling of warmer thermal niches[33,45,46] by the same increasingly dominant species with good dispersal and colonisation capacities[52], which will outweigh species gains through borealisation.

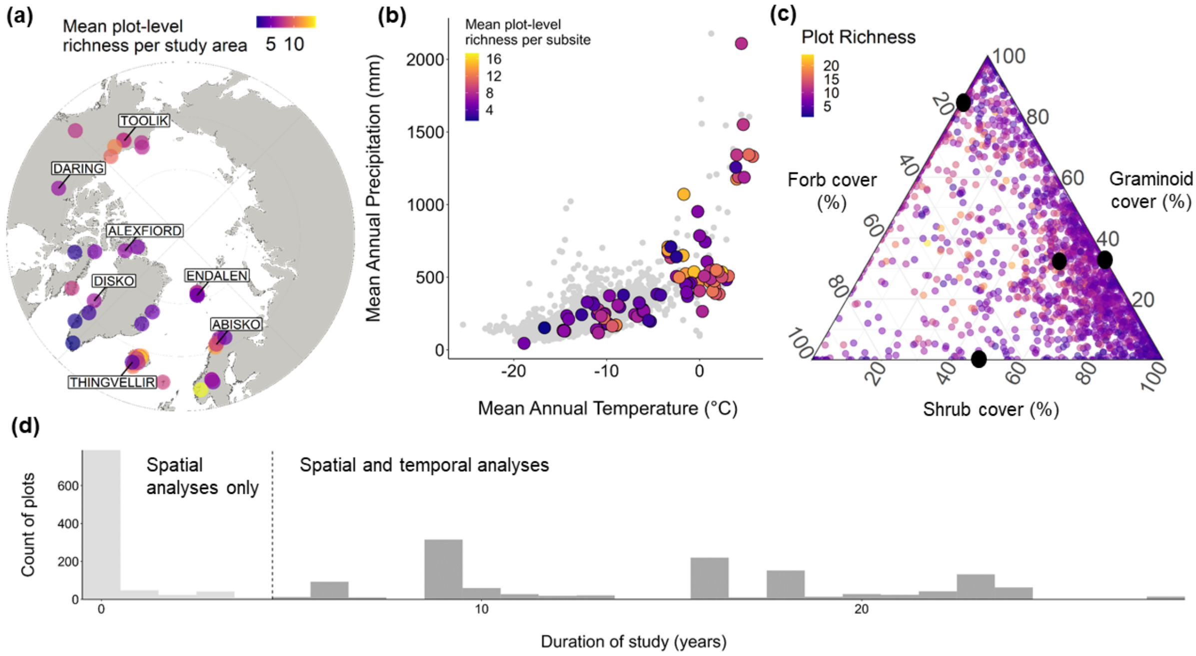

Figure 1. Representation of our dataset within the geographical, climatic and biotic space, and its temporal resolution. a) Distribution of study areas, coloured according to mean plot-level vascular plant richness per study area (*n* = 45). This mean calculation is done for visualisation purposes only, 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[35], 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 S1**.

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 ~one species per every 5° increase at mid-range Arctic latitudes, 97.5% CI = -0.05 to -0.01; **Figure 1a**, **S7**, **Table S2.1**). 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, **Table S2.2**) and in plots with greater forb cover and lower graminoid cover (**Figure 1c**, **Table S1**, **S2.4** - **5**). Despite greater plant richness at lower latitudes and warmer sites, Arctic plant richness did not change directionally over time (slope = 0.0021 log(species) year^{-1}, 95% CI = -0.0002 to 0.0043, equating to 0.01 species gain per year; **Figure 2b**, **c**, **Table S3**). Species richness change was not related to latitude (**Figure 2a**, **Table S2.51**), 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). Declines in richness occurred with increasing shrub cover, and particularly where non-dwarf shrubs, but not dwarf shrubs, increased over time (**Figure 2e**, **Table S2.52**, **S2.52b**). 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 S2.53** - **54**). 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 more even experienced fewer plot-level species gains and losses (**Figure S10**).

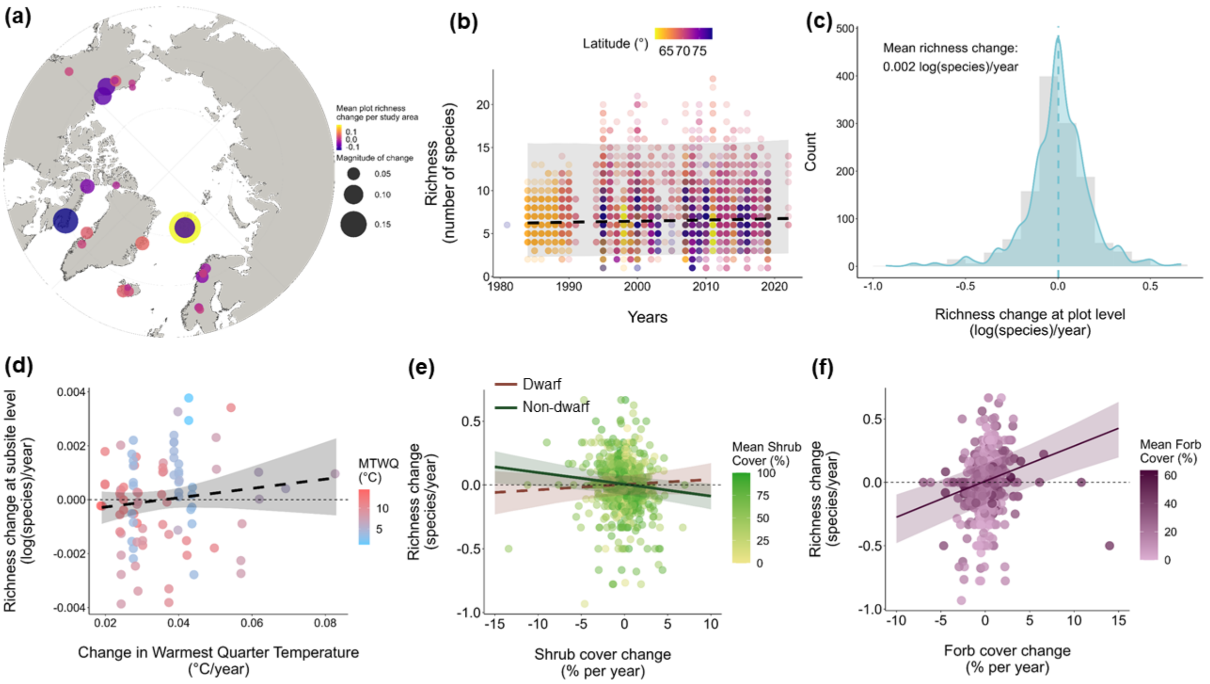

Figure 2. There was no directional change in species richness across the Arctic. a) Richness change values calculated as the mean slope of richness change across all plots in each of the 25 study areas with plots retained for temporal analyses. This average is done for visualisation purposes only, with analyses and estimates of richness change elsewhere calculated at the plot level, unless specified (**Table S2.51**). 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)** Richness did not change directionally over time. Richness is presented per plot and year, coloured according to the latitudinal gradient. The line and band represent the model output from **Table S3**. **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 blue line represents mean richness change. Histogram bin width is 0.1. Model structure and output is in **Table S3**. **d)** Richness did not increase at subsites where long-term warming trends were stronger (warmest quarter temperatures). Points represent richness change slopes at the subsite level (*n* = 90) and are coloured according to climatology (long-term temperature means). **e)** Richness decreased where non-dwarf shrubs (but not dwarf shrubs) increased over time. Points are coloured according to mean shrub cover per plot over time. **f)** Richness increased where forbs increased over time. 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 abundance, with 59% of plots either gaining or losing species (**Figure 3**). Arctic communities experienced a mean temporal turnover of 0.22 (Jaccard) and 0.36 (Bray-Curtis) [data bounded by 0 - 1], representing presence-absence and abundance-related turnover at the plot level, respectively. 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 S2.12**, **16** - **18**). Conversely, greater abundance-related temporal turnover (Bray-Curtis) occurred in warmer sites, regions with weaker warming trends (**Figure 3a**, **b**, **Table S2.24** - **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%) (**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).

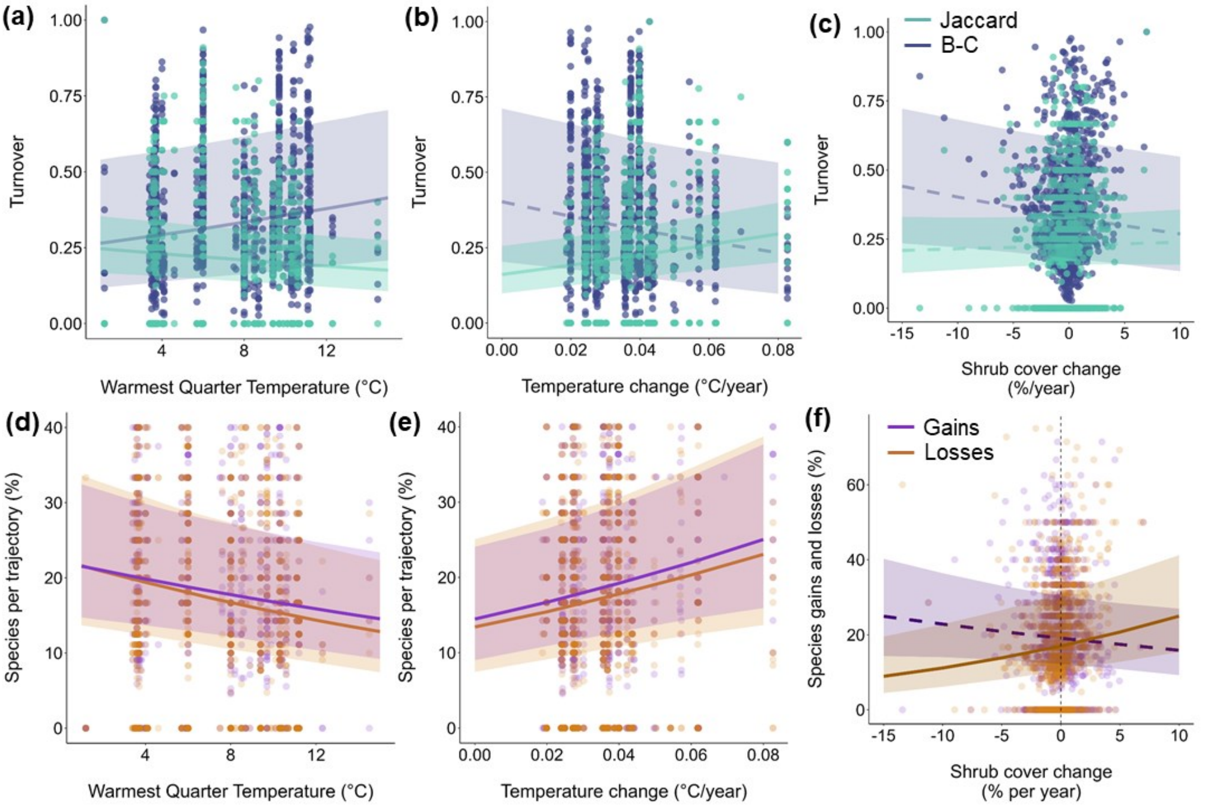

Figure 3. Local climate, climate change and shrubification influenced species' temporal turnover and trajectories. a) Relationships between climate (mean temperature of the warmest quarter, MTWQ)

and two temporal turnover metrics: Jaccard (presence-absence turnover) and Bray-Curtis (presence-absence and abundance turnover). Model outputs are in **Table S2.12**, **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 S2.16** - **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). **c)** Turnover metrics were not directly associated with shrub cover change over time (**Table S2.16**, **21**) **d)** Relationships between MTWQ and species proportion for each trajectory (species gained and lost, persisting species are not displayed). Model outputs are in **Table S2.36**, **44**. **e)** Relationships between MTWQ and species proportion for each trajectory. Model outputs are in **Table S2.40** - **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 S1**, **S2.40**, **48**, **S4**). In all cases, lines represent predicted model fits and bands show the 95% credible intervals. Dashed lines indicate an overall model whose credible intervals 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

There were more persisting species at warmer and drier sites, and more plot-level species losses and gains in colder sites (**Figure 3d**, **Table S2.28**, **36**, **44**). Stronger warming trends were associated with reduced plot-level species persistence and higher plot-level losses and gains over time (**Figure 3e**, **Table S2.32** - **34**, **40** - **42**, **48** - **50**). There were 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 more species gained where forbs had increased (**Table S1**, **S2.40** - **42**). There were fewer species gains where shrubs had increased, but the effect was non-significant (**Figure 3f**, **Table S2.45**). 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 non-dwarf shrubs respond positively to warming (**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**).

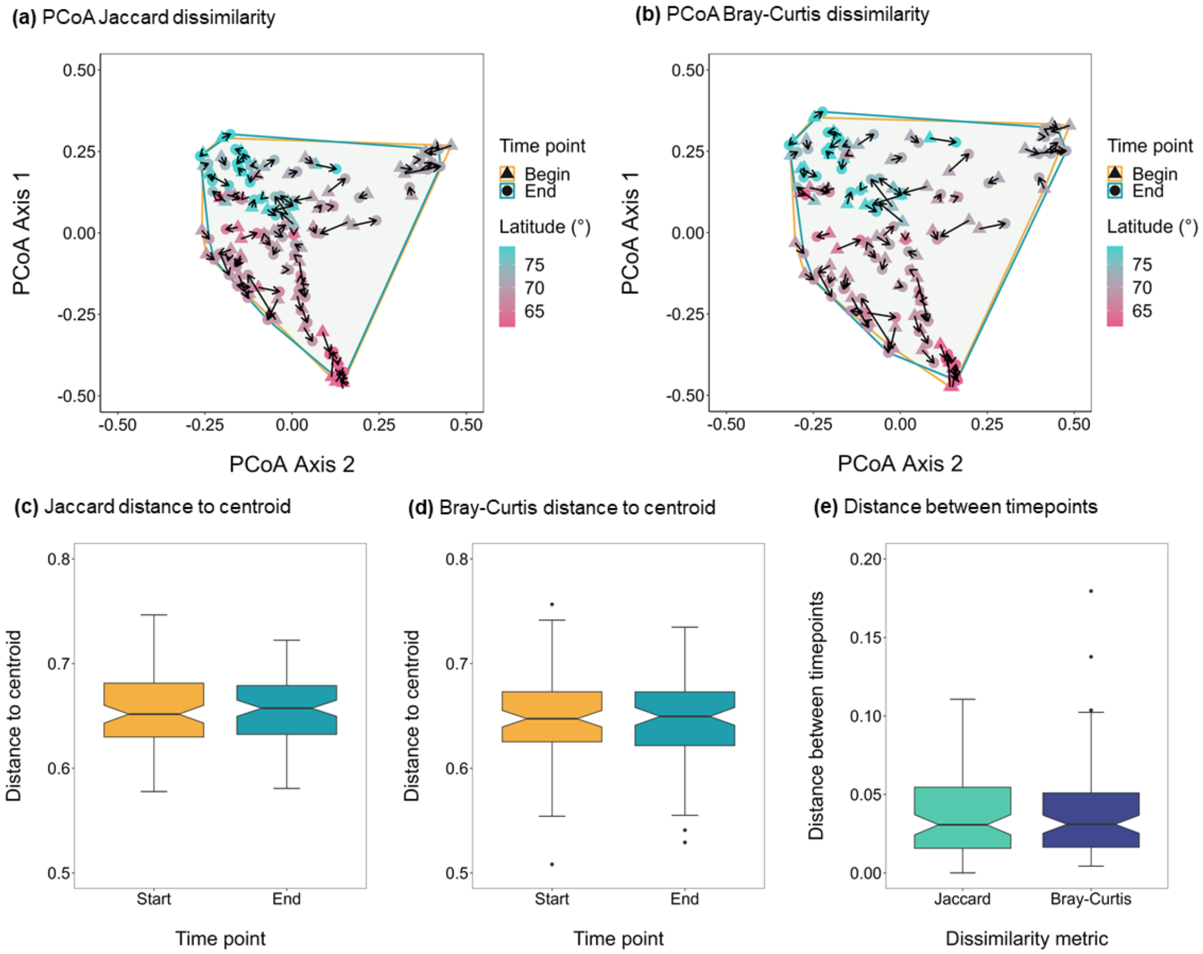

Figure 4. Subsites showed no homogenisation or differentiation over time across the Arctic. We calculated temporal change in spatial turnover (β-diversity) between the start (i.e., baseline) and end (i.e., final) time period for all subsites. Principal Coordinate Analyses (PCoAs) are shown with the **a)** 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

We found that Arctic plant species abundance and composition changed over time (**Figure 3**). However, despite rapid increases in temperatures over the past few decades (**Figure S5b**), we did not find evidence of directional overall plot richness change (α-diversity) over time across the Arctic (**Figure 2b**, **c**). These large-scale results run contrary to literature predictions[19] and contrast with experimental observations of plant diversity declines at the local scale[53] and modelling studies at the regional scale. For example, previous research predicted declines in Arctic-alpine plant species richness of 15 - 47%, with endemic plants being particularly threatened with extinction[21]. Rates of species turnover were greater in warming sites, which experienced higher rates of both species losses and species gains (**Figure 3b**, **3e**). Increases in shrub cover over time were accompanied by decreases in richness and evenness, and greater species losses (**Figure 2e**, **3f**, **Table S1**). We found some evidence for community resistance to rapid Arctic warming, with fewer species losses in plots that were more diverse and even (**Figure S10**). We observed no signs of Arctic-wide subsite homogenisation, with no directional temporal changes in spatial dissimilarity of species composition (**Figure 4**, **S15**), despite widespread compositional change at the plot scale (**Figure 3**). Our findings indicate that Arctic vascular plant communities are responding in a variety of directions due to local idiosyncrasy, and thus comprehensive monitoring at local scales is key to strengthen our large-scale understanding of future Arctic change.

Climate influenced diversity change

Despite spatial species richness being greater at lower latitudes and warmer sites (**Figure S7**, **Table S1**), and rapid Arctic warming over time (**Figure S5b**), the lack of plot richness (α-diversity) change was counter to our expectations (**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., borealization) 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)[20,54]. Species richness increases were not greater at sites with greater rates of warming over time (**Figure 2d**), but warming was associated with greater species gains and losses (**Figure 3e**), possibly due to cold-adapted species not coping with warming, and to warm-adapted species expanding to warmer areas and further displacing cold-adapted species[52,55]. This suggests that plant community composition is being influenced by warming (**Figure 3b**), but that species gains and losses could currently balance each other (**Figure 3e**,

S12), hence resulting in the observed overall non-directional richness change (**Figure 2b**). With 99% of plots experiencing changes in species abundance, and 66% gaining and/or losing species, 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 diversity change

We found that shrubification was associated with richness and compositional change. Shrub expansion has been widely reported[2,4,56], 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 (**Figure S14c**), in agreement with previous pan-Arctic studies[4]. Instead, shrub cover was sensitive to temperature, with non-dwarf shrub cover increasing and dwarf shrub cover decreasing with warmer temperatures (**Figure S14b**). Where shrub cover increased over time, plots experienced decreases in species richness, community evenness, and greater species losses (**Figure 2e**, **3f**, **Table S1**). Lower species richness has been observed with greater shrub cover spatially, with shading and litter production leading to decreases in sun-loving plants under shrub canopies[23,24]. 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[41,57,58]. Thus, Arctic diversity might be more at risk at sites with increasing shrub cover, particularly from tall 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 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[59–61]. Overall, our findings suggest that increased competition from shrubs[61,62] is a main driver of Arctic diversity change.

Resistance to change despite rapid warming

Our findings demonstrate some resistance of Arctic plant richness change (**Figure 2b**, **c**) despite 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 greatest resistance to change, with a lower proportion of species losses and gains (**Figure S10**). While this could be influenced by smaller species pool sizes leading to proportionally greater gains and losses, this result suggests that community resistance could be linked to the reduced extinction risk derived from greater richness and lack of species dominance[42,63]. We found that persistence was more common in locally warm and dry environments, while there were proportionally more species losses in cold sites (**Figure 3c**). Homogenisation has been forecast for High Arctic vegetation[45,46], 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[44], 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[62]. Continued compositional change is likely to lead to additional shifts in plant traits and the functioning of Arctic ecosystems.

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[20,64]. Further research is required to determine whether Arctic ecosystems are indeed exhibiting resistance to warming[65], as other processes could contribute to a lack of detected diversity change. 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 may not yet be detected due to extinction lags[66] and slow colonisation rates in communities of long-lived perennial species. Additionally, priority effects could cause heterogeneity in species responses to warming[67]. Variation in topography, microclimate and nutrient availability could mediate ecological responses and buffer against climate change impacts by providing microhabitats with suitable conditions [68–71]. Thus, the integration of extinction lags, priority effects, and both microand 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[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. Further, the presence or absence of certain bryophytes accurately reflect subtle differences in surface hydrology (e.g., drying versus paludification), soil chemistry, and disturbance[75,76] , which can in turn affect species composition. It remains a priority to expand non-vascular plant surveys to obtain a comprehensive view of plant biodiversity change and biotic interactions among functional groups.

Contrary to our hypotheses, we found no directional trend in vascular plant richness change to date, despite the Arctic experiencing the greatest rates of warming on Earth[1]. Taken together, we find that Arctic composition and richness change are decoupled, with no net richness change despite widespread plant 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 tall shrub increases[2,23]. Despite the lack of a strong relationship between warming and richness change, both 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 decreased species richness and increased species losses where shrub cover increased the most over time (**Figure 2**, **3**). We did not find evidence of homogenisation of Arctic vascular plant communities over time (**Figure 4**), indicating resistance of plant communities to rapid change thus far. Overall, our findings indicate that likely pathways of Arctic plant diversity change include colonisations from local species pools[20], losses of cold-adapted species[55], gains of thermophilous species[52] and increased competition with canopy-forming shrubs[23]. This reshuffling of Arctic vascular plant composition in recent decades could be the precursor of future biodiversity change to come, with impacts on ecosystem function, wildlife habitats, and livelihoods for Arctic people[5,6].

Methods

Plant composition data

We extracted composition and abundance data from the International Tundra Experiment (ITEX+) dataset[77,78]. 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.

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[17,62]. 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.

Plots range in size (i.e., surface area) based on the plant species community of interest and landscape characteristics[77,79] (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**). 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 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)[62]. 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[80–82]. 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 according to the species-area relationship[83].

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 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 (**Table S1**). Plots without a particular functional group present neither at the start or the end were discarded from this analysis. 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)[84] 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 only MTWQ (hereafter 'temperature') as it best represents the growing season conditions and has been previously linked to plant biomass, growth and reproductive rates[85–87], 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 – 2013. 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 to perform better predicting precipitation patterns[84,88,89].

Biodiversity metrics

We chose to analyse common biodiversity metrics that capture species diversity, dominance, and composition change, rather than composite indices, in order to understand 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[90], 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[91].

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 for modelling. Species proportions were calculated by dividing the number of species per trajectory in a plot by the total number of species in each plot (including losses, gains and persisting species).

Statistical analyses

We employed a Bayesian framework for all analyses. We used the software and programming language R version 4.1.0[92]. Models were fitted using the 'brms' package[93] and ran for as many iterations as necessary to achieve convergence, which was assessed through examination of the R_{hat} term and trace plots.

Model types

We fitted three main types of models: spatial, two time-point and temporal (**Table S1**). 1) 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. These models identify the main drivers behind spatial patterns of plant diversity. 2) 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).

3) 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 these temporal models (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); 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 (**Table S1**). 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 and for each response variable, we fitted several models (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 S1**, **S2**). We used a hierarchical modelling approach by including a subsite random effect (as random intercepts) to account for non-independence of plots within subsites.

Additional models

For all temporal metrics (i.e., temporal models and two time-point models), we retained those plots with a minimum of two sampling points and at least five years of monitoring duration. 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 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 S5**). 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.

Calculation of covariates

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**). 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 calculated change over time in temperature and precipitation by fitting linear models of yearly climatic values over the 1978 - 2013 period, and used the slopes of change per plot as fixed variables in the models (as MTWQ and precipitation change, **Table S1**). 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.

Sampling design covariates

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[83,91]. The covariates of functional group proportions and richness were calculated as the mean values across all years to reflect the most common conditions in a plot over time (**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 S4**).

Data families

We fitted hierarchical models with different response distributions depending on the structure of the response variable (**Table S1**). These included Gaussian with an identity link function (for response metrics with a normal distribution), negative binomial with a log link function (for count data where the variance is greater than the mean), beta with a logit link function (for values between 0 - 1, excluding 0 and 1), zero-inflated beta with a logit link function (for values between 0 and 0.99), and zero-one-inflated beta with a logit link function (for values between 0 - 1, including 0 and 1). For beta families, 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). We specified weakly informative priors for beta and negative binomial families.

Posthoc 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[4,94]. 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 non-dwarf). Additionally, we modelled shrub cover change per plot as a function of long-term temperature change (over the 1978 - 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.[95] and categorised shrubs as dwarf and non-dwarf (including low and tall shrubs), since we were interested in the ecological effects of species sprawling versus erect physiognomy.

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'[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 90 subsites (**Figure S15**). 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 Arctic An overall decrease in this distance across all subsites would indicate compositional homogenisation.

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

References

1. IPCC. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. (2021).

2. Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change **2**, 453–457 (2012).

3. Myers-Smith, I. H. & Hik, D. S. Climate warming as a driver of tundra shrubline advance. Journal of Ecology **106**, 547–560 (2017).

4. García Criado, M., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E. R. & Stevens, N. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. Global Ecology and Biogeography **29**, 925–943 (2020).

5. Wookey, P. A. et al. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Global Change Biology **15**, 1153–1172 (2009).

6. Hamilton, C. W. et al. Predicting the suitable habitat distribution of berry plants under climate change. Landsc Ecol **39**, 18 (2024).

7. Díaz, S., Settele, J. & Brondízio, E. Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. (IPBES, 2019).

8. Antão, L. H. et al. Temperature-related biodiversity change across temperate marine and terrestrial systems. Nature Ecology & Evolution **4**, 927–933 (2020).

9. Butchart, S. H. M. et al. Global Biodiversity: Indicators of Recent Declines. Science **328**, 1164–1168 (2010).

10. Pereira, H. M. et al. Scenarios for Global Biodiversity in the 21st Century. Science **330**, 1496–1501 (2010).

11. van der Plas, F. et al. Biotic homogenization can decrease landscape-scale forest multifunctionality. PNAS **113**, 3557–3562 (2016).

12. Savage, J. & Vellend, M. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography **38**, 546–555 (2015).

13. Blowes, S. A. et al. The geography of biodiversity change in marine and terrestrial assemblages. Science **366**, 339–345 (2019).

14. Dornelas, M. et al. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science **344**, 296–299 (2014).

15. Freeman, B. G., Song, Y., Feeley, K. J. & Zhu, K. Montane species track rising temperatures better in the tropics than in the temperate zone. Ecology Letters **24**, 1697–1708 (2021).

16. Bjorkman, A. D. et al. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. Ambio (2019) doi:10.1007/s13280-019-01161-6.

17. Valdez, J. W. et al. The undetectability of global biodiversity trends using local species richness. Ecography **2023**, e06604 (2023).

18. Louthan, A. M., Peterson, M. L. & Shoemaker, L. G. Climate sensitivity across latitude: scaling physiology to communities. Trends in Ecology & Evolution **36**, 931–942 (2021).

19. Nabe-Nielsen, J. et al. Plant community composition and species richness in the High Arctic tundra: From the present to the future. Ecology and Evolution **7**, 10233–10242 (2017).

20. Daskalova, G. N. & et al. Dark diversity in the tundra: the source of future biodiversity change? (In prep.).

21. Niskanen, A. K. J., Niittynen, P., Aalto, J., Väre, H. & Luoto, M. Lost at high latitudes: Arctic and endemic plants under threat as climate warms. Diversity and Distributions **25**, 809–821 (2019).

22. Elmendorf, S. C. & Hollister, R. D. Limits on phenological response to high temperature in the Arctic. Sci Rep **13**, 208 (2023).

23. Pajunen, A. M., Oksanen, J. & Virtanen, R. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. Journal of Vegetation Science **22**, 837–846 (2011).

24. Boscutti, F. et al. Shrub growth and plant diversity along an elevation gradient: Evidence of indirect effects of climate on alpine ecosystems. PLOS ONE **13**, e0196653 (2018).

25. von Humboldt, A. & Bonpland, A. The Geography of Plants. (1807).

26. Hillebrand, H. On the generality of the latitudinal diversity gradient. Am Nat **163**, 192–211 (2004).

27. Saupe, E. E. et al. Spatio-temporal climate change contributes to latitudinal diversity gradients. Nat Ecol Evol **3**, 1419–1429 (2019).

28. Post, E., Steinman, B. A. & Mann, M. E. Acceleration of phenological advance and warming with latitude over the past century. Sci Rep **8**, 3927 (2018).

29. Steinbauer, M. J. et al. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature **556**, 231 (2018).

30. Wipf, S., Stöckli, V., Herz, K. & Rixen, C. The oldest monitoring site of the Alps revisited: accelerated increase in plant species richness on Piz Linard summit since 1835. Plant ecology & diversity (2013).

31. Körner, C. Concepts in Alpine Plant Ecology. Plants **12**, 2666 (2023).

32. Brodie, J. F., Roland, C. A., Stehn, S. E. & Smirnova, E. Variability in the expansion of trees and shrubs in boreal Alaska. Ecology **100**, e02660 (2019).

33. Harsch, M. A., Hulme, P. E., McGlone, M. S. & Duncan, R. P. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters **12**, 1040–1049 (2009).

34. Hofgaard, A., Tømmervik, H., Rees, G. & Hanssen, F. Latitudinal forest advance in northernmost Norway since the early 20th century. Journal of Biogeography **40**, 938–949 (2013).

35. Walker, D. A. et al. The Circumpolar Arctic vegetation map. Journal of Vegetation Science **16**, 267–282 (2005).

36. Wisz, M. S. et al. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews **88**, 15–30 (2013).

37. Burrows, M. T. et al. The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. Science **334**, 652–655 (2011).

38. McGraw, J. B. et al. Northward displacement of optimal climate conditions for ecotypes of Eriophorum vaginatum L. across a latitudinal gradient in Alaska. Global Change Biology **21**, 3827–3835 (2015).

39. Chapin, F. S., Bret-Harte, M. S., Hobbie, S. E. & Zhong, H. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science **7**, 347–358 (1996).

40. Prager, C. M. et al. A mechanism of expansion: Arctic deciduous shrubs capitalize on warming-induced nutrient availability. Oecologia **192**, 671–685 (2020).

41. Walker, M. D. et al. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America **103**, 1342–1346 (2006).

42. Hillebrand, H., Bennett, D. M. & Cadotte, M. W. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. Ecology **89**, 1510–1520 (2008).

43. Frishkoff, L. O. et al. Climate change and habitat conversion favour the same species. Ecology Letters **19**, 1081–1090 (2016).

44. Blowes, S. A. et al. Synthesis reveals approximately balanced biotic differentiation and homogenization. Science Advances **10**, eadj9395 (2024).

45. Niittynen, P., Heikkinen, R. K. & Luoto, M. Decreasing snow cover alters functional composition and diversity of Arctic tundra. PNAS **117**, 21480–21487 (2020).

46. Stewart, L., Simonsen, C. E., Svenning, J.-C., Schmidt, N. M. & Pellissier, L. Forecasted homogenization of high Arctic vegetation communities under climate change. Journal of Biogeography **45**, 2576–2587 (2018).

47. Kitagawa, R. et al. Positive interaction facilitates landscape homogenization by shrub expansion in the forest–tundra ecotone. Journal of Vegetation Science **31**, 234–244 (2020).

48. Naito, A. T. & Cairns, D. M. Patterns of shrub expansion in Alaskan arctic river corridors suggest phase transition. Ecology and Evolution **5**, 87–101 (2015).

49. van der Kolk, H. J., Heijmans, M., van Huissteden, J., Pullens, J. W. M. & Berendse, F. Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw. Biogeosciences **13**, 6229–6245 (2016).

50. Holtmeier, F. & Broll, G. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography **14**, 395–410 (2005).

51. Lawrence, E. R. & Fraser, D. J. Latitudinal biodiversity gradients at three levels: Linking species richness, population richness and genetic diversity. Global Ecology and Biogeography **29**, 770–788 (2020).

52. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change. Nature Climate Change **2**, 111–115 (2012).

53. Post, E. et al. Large herbivore diversity slows sea ice–associated decline in arctic tundra diversity. Science **380**, 1282–1287 (2023).

54. Trindade, D. P. F., Carmona, C. P. & Pärtel, M. Temporal lags in observed and dark diversity in the Anthropocene. Global Change Biology **26**, 3193–3201 (2020).

55. Elmendorf, S. C. et al. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. PNAS **112**, 448–452 (2015).

56. Myers-Smith, I. H. et al. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. **6**, 045509 (2011).

57. Scharnagl, K., Johnson, D. & Ebert-May, D. Shrub expansion and alpine plant community change: 40-year record from Niwot Ridge, Colorado. Plant Ecology & Diversity **12**, 407–416 (2019).

58. Wallace, C. A. & Baltzer, J. L. Tall Shrubs Mediate Abiotic Conditions and Plant Communities at the Taiga–Tundra Ecotone. Ecosystems **23**, 828–841 (2020).

59. Klanderud, K., Vandvik, V. & Goldberg, D. The Importance of Biotic vs. Abiotic Drivers of Local Plant Community Composition Along Regional Bioclimatic Gradients. PLOS ONE **10**, e0130205 (2015).

60. Liu, H. et al. Shifting plant species composition in response to climate change stabilizes grassland primary production. PNAS **115**, 4051–4056 (2018).

61. Bråthen, K. A., Pugnaire, F. I. & Bardgett, R. D. The paradox of forbs in grasslands and the legacy of the mammoth steppe. Frontiers in Ecology and the Environment **19**, 584–592 (2021).

62. Bjorkman, A. D. et al. Plant functional trait change across a warming tundra biome. Nature **562**, 57 (2018).

63. Wilsey, B. J. & Polley, H. W. Realistically Low Species Evenness Does Not Alter Grassland Species-Richness–Productivity Relationships. Ecology **85**, 2693–2700 (2004).

64. Speed, J. D. M. et al. Will borealization of Arctic tundra herbivore communities be driven by climate warming or vegetation change? Global Change Biology **27**, 6568–6577 (2021).

65. Van Meerbeek, K., Jucker, T. & Svenning, J.-C. Unifying the concepts of stability and resilience in ecology. Journal of Ecology **109**, 3114–3132 (2021).

66. Lenoir, J. et al. Species better track climate warming in the oceans than on land. Nat Ecol Evol **4**, 1044–1059 (2020).

67. Ke, P.-J. & Letten, A. D. Coexistence theory and the frequency-dependence of priority effects. Nat Ecol Evol **2**, 1691–1695 (2018).

68. Scharn, R. et al. Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra. Environ. Res. Lett. **16**, 064031 (2021).

69. Graae, B. J. et al. Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. Perspectives in Plant Ecology, Evolution and Systematics **30**, 41–50 (2018).

70. Lembrechts, J. J. et al. Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. Ecography **41**, 900–909 (2018).

71. Ropars, P. & Boudreau, S. Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography. Environ. Res. Lett. **7**, 015501 (2012).

72. Lett, S. et al. Can bryophyte groups increase functional resolution in tundra ecosystems? Arctic Science 1–29 (2021) doi:10.1139/as-2020-0057.

73. Soudzilovskaia, N. A. et al. How do bryophytes govern generative recruitment of vascular plants? New Phytologist **190**, 1019–1031 (2011).

74. Mallen-Cooper, M., Graae, B. J. & Cornwell, W. K. Lichens buffer tundra microclimate more than the expanding shrub Betula nana. Annals of Botany **128**, 407–418 (2021).

75. Forbes, B. C. The importance of bryophytes in the classification of human-disturbed high arctic vegetation. Journal of Vegetation Science **5**, 877–884 (1994).

76. Forbes, B. C. Tundra Disturbance Studies, III: Short-term Effects of Aeolian Sand and Dust, Yamal Region, Northwest Siberia. Environmental Conservation **22**, 335–344 (1995).

77. Bjorkman, A. D. The ITEX+ composition database: Thirty years of experimental warming and monitoring of tundra plant communities. (in prep).

78. Henry, G. H. R. et al. The International Tundra Experiment (ITEX): 30 years of research on tundra ecosystems. Arctic Science **8**, 550–571 (2022).

79. Prevéy, J. S. et al. Warming shortens flowering seasons of tundra plant communities. Nature Ecology & Evolution **3**, 45–52 (2019).

80. Ray, N. & Adams, J. A GIS-based vegetation map of the world at the Last Glacial Maximum (25,000-15,000 BP). Internet Archaeology **11**, (2001).

81. Abbott, R. J. & Brochmann, C. History and evolution of the arctic flora: in the footsteps of Eric Hultén. Molecular Ecology **12**, 299–313 (2003).

82. Zhang, J. et al. Evolutionary history of the Arctic flora. Nat Commun **14**, 4021 (2023).

83. Drakare, S., Lennon, J. J. & Hillebrand, H. The imprint of the geographical, evolutionary and ecological context on species–area relationships. Ecology Letters **9**, 215–227 (2006).

84. Karger, D. N. et al. Climatologies at high resolution for the earth’s land surface areas. Scientific Data **4**, (2017).

85. van der Wal, R. & Stien, A. High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. Ecology **95**, 3414–3427 (2014).

86. Rayback, S. A. & Henry, G. H. R. Dendrochronological Potential of the Arctic Dwarf-Shrub Cassiope tetragona. Tree-Ring Research **61**, 43–53 (2005).

87. Weijers, S., Broekman, R. & Rozema, J. Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub Cassiope tetragona. Quaternary Science Reviews **29**, 3831–3842 (2010).

88. Maria, B. & Udo, S. Why input matters: Selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. Ecological Modelling **359**, 92–102 (2017).

89. Datta, A., Schweiger, O. & Kühn, I. Origin of climatic data can determine the transferability of species distribution models. NB **59**, 61–76 (2020).

90. Gotelli, N. J. & Colwell, R. K. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**, 379–391 (2001).

91. Rosenzweig, M. L. Species Diversity in Space and Time. (Cambridge University Press, Cambridge, 1995). doi:10.1017/CBO9780511623387.

92. R Core Team. R: A Language and Environment for Statistical Computing. https://www.R-project.org/ (2021).

93. Bürkner, P.-C. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software **80**, 1–28 (2017).

94. Myers-Smith, I. H. et al. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change **5**, 887–891 (2015).

95. García Criado, M. et al. Plant traits poorly predict winner and loser shrub species in a warming tundra biome. Nat Commun **14**, 3837 (2023).

96. Oksanen, J. et al. vegan: Community Ecology Package. R package version 2.5-7. (2020) doi:https://CRAN.R-project.org/package=vegan.

97. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics **35**, 526–528 (2019).

98. Anderson, M. J. et al. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters **14**, 19–28 (2011).

99. Anderson, M. J., Ellingsen, K. E. & McArdle, B. H. Multivariate dispersion as a measure of beta diversity. Ecology Letters **9**, 683–693 (2006).