Functional diversity of tundra vascular plants over space and time

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Joseph J. Everest, Isla H. Myers-Smith, Mariana García Criado, Anne D. Bjorkman, Hannah S. Wauchope, Mark Vellend, Jonathan Lenoir, Robert G. Björk, Marko J. Spasojevic, Elina M. Kaarlejärvi, Alison L. Beamish, Juha M. Alatalo, Alba Anadon-Rosell, Lander Baeten, Yang Bai, Logan T. Berner, Katlyn R. Betway-May, Mats P. Björkman, Noémie Boulanger-Lapointe, Allan Buras, Michele Carbognani, Katherine Sarah Christie, Elisabeth J. Cooper, Stefan Dullinger, Bo Elberling, Anu Eskelinen, Bruce C. Forbes, Esther R. Frei, William A. Gould, Oriol Grau, Peter T. Green, Paul Grogan, Sylvia Haider, Konsta Happonen, Luise Hermanutz, Rebecca E. Hewitt, Robert D. Hollister, Karl Hülber, Maitane Iturrate-Garcia, Ingibjörg S. Jónsdóttir, Saewan Koh, Tiina H. M. Kolari, Laurent J. Lamarque, Nicolas Lecomte, Jonas J. Lembrechts, Esther Lévesque, Robert J. Lewis, Miska Luoto, Petr Macek, Michelle C. Mack, Jeremy L. May, Julie Messier, Robert Muscarella, Josep M. Ninot, Signe Normand, Johan Olofsson, Vladimir G. Onipchenko, Matteo Petit Bon, Alessandro Petraglia, Eric Post, Janet S. Prevéy, Riikka Rinnan, Christian Rixen, Sabine B. Rumpf, Ingvild Ryde, Gabriela Schaepman-Strub, Franziska Schrodt, Josep M. Serra-Diaz, Rohan H. Shetti, Nadejda A. Soudzilovskaia, James D. M. Speed, Mariska te Beest, Anne Tolvanen, Andrew Trant, Urs Albert Treier, Susanna E. Venn, Anna-Maria Virkkala, Tage Vowles, Martin Wilmking, and Sarah C. Elmendorf

Author Details:

Joseph J. Everest (Corresponding Author)
joseph.j.everest@gmail.com
- Global Change Research Institute, School of GeoSciences, University of Edinburgh
- RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

Isla H. Myers-Smith
- Global Change Research Institute, School of GeoSciences, University of Edinburgh
- Department of Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver Campus

Mariana García Criado
- Global Change Research Institute, School of GeoSciences, University of Edinburgh
- CREAF, Bellaterra (Cerdanyola del Vallès), Spain

Anne D. Bjorkman
- Department of Biological & Environmental Sciences, University of Gothenburg, Medicinaregatan 7B, 413 90 Gothenburg

Hannah S. Wauchope
- Global Change Research Institute, School of GeoSciences, University of Edinburgh

Mark Vellend
- Département de biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke, Québec, Canada, J1K 2R1

Jonathan Lenoir

- UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, 80000 Amiens, France

Robert G. Björk
- Department of Earth Sciences, University of Gothenburg, SE-405 30 Gothenburg, Sweden.
- Gothenburg Global Biodiversity Centre, University of Gothenburg, SE-405 30 Gothenburg, Sweden.

Marko J. Spasojevic
- Department of Ecology, Evolution, & Organismal Biology, University of California–Riverside, Riverside, CA

Elina M. Kaarlejärvi
- Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, FI-00014 University of Helsinki, Finland

Alison L. Beamish
- Department of Geodesy, Section of Remote Sensing and Geoinformatics Helmholtz Centre Potsdam – German Centre for Geosciences (GFZ), Germany

Juha M. Alatalo
- Environmental Science Center, Qatar University

Alba Anadon-Rosell
- CREAF, Edifici C, Campus UAB, 08193 Cerdanyola del Vallès, Spain

Lander Baeten
- Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267 B-9090 Gontrode

Yang Bai
- Center for Integrative Conservation & Yunnan Key Laboratory for Conservation of Tropical Rainforests and Asian Elephants, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, 666303, China

Logan T. Berner
- School of Informatics, Computing, and Cyber Systems, Northern Arizona University, 1295 S. Knoles Drive, Flagstaff, Arizona USA 86011

Katlyn R. Betway-May
- US Forest Service, US Department of Agriculture, Río Piedras, PR, USA

Mats P. Björkman
- Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, SE- 405 30 Gothenburg, Sweden.
- Gothenburg Global Biodiversity Centre, University of Gothenburg, Box 463, SE- 405 30 Gothenburg, Sweden.

Noémie Boulanger-Lapointe
- Department of Geography, University of Victoria, 3800 Finnerty Road, Victoria, BC V8P 5C2

Allan Buras
- Land Surface-Atmosphere Interactions, TU Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

Michele Carbognani
- University of Parma, Dept. of Chemistry, Life Sciences and Environmental Sustainability. Parco Area delle Scienze 11/A, 43124 Parma, Italy

Katherine Sarah Christie
- Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK, 99518

Elisabeth J. Cooper
- Department of Arctic and Marine Biology, Faculty of Biosciences Fisheries and Economics, UiT-The Arctic University of Norway, N-9037 Tromsø, Norway

Stefan Dullinger
- Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna

Bo Elberling
- Department of Geosciences and Natural Resource Management University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K. DENMARK

Anu Eskelinen
- Ecology and Genetics Unit, University of Oulu, P.O. Box 8000, FI-90014 University of Oulu, Finland

Bruce C. Forbes
- Arctic Centre, University of Lapland, FI-96101 Rovaniemi, Finland

Esther R. Frei
- Alpine Environment and Natural Hazards, WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, 7260 Davos Dorf, Switzerland

William A. Gould
- USDA Forest Service 1201 Calle Ceiba, San Juan, PR 00926

Oriol Grau
- Research Observatory of the Alt Pirineu Natural Park / Carrer de la Riba 1, 25595, Llavorsí, Catalonia, Spain

Peter T. Green
- Department of Environment and Genetics and Research Centre for Future Landscapes, La Trobe University, Melbourne, Australia

Paul Grogan
- Department of Biology, Biosciences Complex, 116 Arch Street, Kingston, ON K7L 3N6, Canada

Sylvia Haider
- Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany

Konsta Happonen
- Finnish Youth Research Society, Kumpulantie 3, 00520 Helsinki, Finland

Luise Hermanutz
- Dept of BIology, Memorial University, St. John's, NL

Rebecca E. Hewitt

- Amherst College, Department of Environmental Studies, Amherst, Massachusetts 01002

Robert D. Hollister
- Biology Department, Grand Valley State University, Allendale, Michigan, USA

Karl Hülber
- Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-1030 Vienna, Austria

Maitane Iturrate-Garcia
- Department of Metrology in Chemistry and Biology, Federal Institute of Metrology (METAS), Bern-Wabern 3003, Switzerland

Ingibjörg S. Jónsdóttir
- Institute of Life and Environmental Sciences, University of Iceland, 102 Reykjavik, Iceland

Saewan Koh
- University of Toronto, Faculty of Applied Science and Engineering. 35 St. George St. Toronto, Ontario, Canada M5S 1A4

Tiina H. M. Kolari
- Centre de recherche sur la dynamique du système Terre (GEOTOP), Université du Québec à Montréal, 201 Président-Kennedy Avenue, Montréal QC, H2X 3Y7, Canada

Laurent J. Lamarque
- Département des Sciences de l’environnement et Centre d’études nordiques, Université du Québec à Trois-Rivières, Trois-Rivières, Québec, Canada

Nicolas Lecomte
- Canada Research Chair in Polar and Boreal Ecology and Centre d'Études Nordiques, Département de Biologie, Université de Moncton, Moncton, New Brunswick, Canada E1A 3E9

Jonas J. Lembrechts
- Utrecht University, P.O. Box 800.56, 3508 TB, Utrecht, the Netherlands

Esther Lévesque
- Département des Sciences de l'environnement et Centre d'études nordiques, Université du Québec à Trois-Rivières, Trois-Rivières, Qc, Canada, G8Z 4M3

Robert J. Lewis
- Norwegian Institute for Nature Research

Miska Luoto
- Department of Geosciences and Geography, P.O. Box 64 (Gustaf Hällströmin katu 2), FI-00014 University of Helsinki, Finland

Petr Macek
- Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, Na Sadkach 7, Ceske Budejovice 370 05, Czech Republic
- Chair of Biodiversity and Nature Tourism, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5a, Tartu 51006, Estonia

Michelle C. Mack

- Center for Ecosystem Science and Society and the Department of Biological Sciences, Northern Arizona University, PO Box 5620, Flagstaff, AZ 86011

Jeremy L. May
- Department of Biology and Environmental Science, Marietta College, 315 5th Street Marietta, OH 45750

Julie Messier
- Biology Department University of Waterloo 200 University Ave. W Waterloo, Ontario, Canada N2L 3G1

Robert Muscarella
- Plant Ecology and Evolution, Uppsala University; Kåbovägen 4, hus 7 752 36 Uppsala, Sweden

Josep M. Ninot
- Institute or Research for Biodiversity (IRBio) and Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona. Av. Diagonal 643, 08028 Barcelona, Spain

Signe Normand
- Department of Biology, Aarhus University, Denmark

Johan Olofsson
- Umeå University

Vladimir G. Onipchenko
- Moscow Lomonosov State University, Leninskie Gory 1 str.12, Moscow, Russia

Matteo Petit Bon
- Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322, USA
- Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695, USA

Alessandro Petraglia
- Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/A, 43124, Parma, Italy

Eric Post
- Department of Wildlife, Fish, and Conservation Biology, University of California Davis, 95616 USA

Janet S. Prevéy
- U.S. Geological Survey, Fort Collins Science
- WSL Institute for Snow and Avalanche Research SLF, Switzerland Center, 2150 Centre Avenue, Building C, Fort Collins, CO, 80526, USA

Riikka Rinnan
- University of Copenhagen, Department of Biology

Christian Rixen
- WSL Institute for Snow and Avalanche Research SLF, Davos, Switzerland
- Climate Change, Extremes and Natural Hazards in Alpine Regions Research Centre CERC, Davos Dorf, Switzerland

Sabine B. Rumpf
- Department of Environmental Sciences, University of Basel, Switzerland. Adress: Bernoullistrasse 32, 4056 Basel

Ingvild Ryde

- Terrestrial Ecology section, Department of Biology, University of Copenhagen

Gabriela Schaepman-Strub

- Dept. Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland

Franziska Schrodt

- University of Nottingham, School of Geography, University Park, Ng7 2RS, Nottingham, UK

Josep M. Serra-Diaz

- Institut Botànic de Barcelona (IBB), CSIC-Ajuntament de Barcelona, Barcelona, Spain
- Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France
- Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

Rohan H. Shetti

- "The Green Concept: Institute for Carbon Assessment and Restoration Ecology, Dr Ketkar Road, 101 Mohar Apartments, Pune, 411004 India"

Nadejda A. Soudzilovskaia

- Centre for Environmental Sciences (CMK), Hasselt University; Martelarenlaan 42; 3500 Hasselt, Belgium

James D. M. Speed

- Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway

Mariska te Beest

- Copernicus Institute of Sustainable Development, Utrecht University, 3584 CB, Utrecht, the Netherlands.
- Centre for African Conservation Ecology, Nelson Mandela University, Gqeberha, 6031, South Africa

Anne Tolvanen

- Natural Resources Institute Finland

Andrew Trant

- School of Environment, Resources and Sustainability; University of Waterloo; 200 University Avenue West, Waterloo, Ontario, Canada N2L 3G1

Urs Albert Treier

- Section for Ecoinformatics & Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark

Susanna E. Venn

- School of Life and Environmental Sciences, Deakin University, 221 Burwood Hwy, Burwood, Victoria, 3125 AUSTRALIA

Anna-Maria Virkkala

- Woodwell Climate Research Center, 149 Woods Hole Rd, Falmouth, MA 02540, United States

Tage Vowles

- IVL Swedish Environmental Research Institute, Box 530 21, 400 14 Göteborg

Martin Wilmking

- Institute for Botany and Landscape Ecology, Greifswald University, Soldmannstrasse 15, D - 17487 Greifswald, Germany

Sarah C. Elmendorf

- Institute of Arctic and Alpine Research, University of Colorado, 4001 Discovery Drive, Boulder, CO 80303 USA

0 Abstract

Aim:

Rapid warming across the tundra biome is driving widespread changes in vascular plant community composition. While species turnover is well-documented, the ramifications for tundra functional diversity are unknown. Here, we quantify biome-scale spatial gradients and temporal trends in the functional diversity of tundra vegetation for the first time.

Location:

A biome-scale synthesis of in situ vegetation surveys and resurveys from 2087 plots across 45 sites throughout the high-latitude tundra.

Time Period:

1984-2022

Major Taxa Studied:

352 vascular plant species encompassing shrub, graminoid and forb functional groups

Methods:

We used tundra species trait data alongside long-term, plot-based sampling of species composition to estimate three functional diversity metrics: functional richness, functional evenness and functional dispersion. We used Bayesian mixed-models to test for latitudinal gradients in functional diversity, temporal trends in functional diversity and major abiotic and biotic correlates of functional diversity over space and time.

Results:

Mirroring biogeographic gradients in species diversity, functional richness declined at high latitude and colder sites. However, functional richness exhibited no net directional change across the three-decade study period. Plots dominated by single growth forms had reduced functional diversity when compared with plots where individual growth forms had intermediate abundance. Changes in temperature and precipitation were not linked to temporal changes in functional diversity. Where shrubs were increasing in abundance, functional richness and dispersion declined, whereas increases in forbs were accompanied by increases in both aspects of functional diversity.

Main Conclusions:

The functional diversity of tundra plants is currently lowest in colder and high latitude sites. Despite rapid warming of the tundra biome, we have yet to see broad-scale changes in functional diversity over time. However, where shrubification occurs, we anticipate accompanying reductions in functional diversity. Our results highlight the potential consequences of changes in tundra species composition for ecosystem functioning over the coming decades.

1 Introduction

Changes to vascular plant communities are widespread throughout the northern latitudes in response to rapid climatic change (Masson-Delmotte et al., 2021; Rantanen et al., 2022). These changes include shifts in the dominance and distribution of certain species and functional traits within tundra communities (Bjorkman et al., 2018a; Elmendorf et al., 2012b, 2015; García Criado et al., 2020, 2023, 2025b; Myers-Smith et al., 2019; Myers-Smith and Hik, 2017; Niittynen et al., 2020; Thomas et al., 2020). The range, variability and evenness of such traits, termed ‘functional diversity’ (Villéger et al., 2008), can alter key ecosystem functions and services (Díaz and Cabido, 2001; Hagan et al., 2023; Häger and Avalos, 2017; Lavorel et al., 2007; Miedema Brown and Anand, 2022; Niittynen et al., 2020; Ottoy et al., 2017; van der Plas et al., 2020; Zylstra et al., 2016). Communities with higher functional diversity could be more stable and have higher capacity to resist global change impacts (Niittynen et al., 2020; but see Lipoma et al., 2024). Consequently, a loss of tundra functional diversity could have cascading effects on ecosystem services, threatening their regulation and long-term persistence (Callaghan et al., 2011; Imbert et al., 2021). Despite the potential importance of functional diversity, it has yet to be quantified across the tundra biome. We addressed this gap through a biome-wide, multi-site synthesis of plot-level functional diversity.

Macroecology provides a theoretical basis for broad-scale latitudinal gradients in diversity. The latitudinal diversity gradient in species richness has been recognised for more than two centuries (Lamanna et al., 2014; Oliveira et al., 2016; Pianka, 1966). Contemporary species richness declines monotonically from the tropics to the tundra (Edie et al., 2018; Mannion et al., 2014), and also across latitude within the tundra biome (García Criado et al., 2025b). However, the relationship of functional diversity with latitude, at least in the tundra, remains unclear. In the tropical and temperate biomes, biogeographic patterns in functional diversity closely follow those of species richness. Functional richness (the volume of trait space filled by species; Mouchet et al., 2010; Villéger et al., 2008) declines with increasing latitude due to a progressive loss of species and corresponding traits. This is thought to lead to a narrowing of functional diversity towards the poles (Edie et al., 2018; Lamanna et al., 2014). In contrast, more environmentally benign conditions at lower latitudes facilitate higher species richness, with many species performing similar functions and occupying the same regions of trait space (Edie et al., 2018; Pastore et al., 2021). These communities tend to have low functional evenness (how evenly abundance is distributed across trait space; Mouchet et al., 2010; Villéger et al., 2008) whilst functional redundancy (the degree to which multiple species occupy similar positions in trait space) tends to be high (Halpern and Floeter, 2008; Oliveira et al., 2016). With the loss of species towards higher, colder latitudes, species are disproportionately lost from oversaturated areas of trait space, reducing redundancy and increasing functional evenness (Edie et al., 2018; Schumm et al., 2019).

Functional diversity in tundra ecosystems may be influenced by both abiotic and biotic factors (Speed et al., 2019). Globally, temperature is likely a major abiotic determinant of biome-scale distributions of tundra functional diversity (Edie et al., 2018; Schumm et al., 2019). The influence of precipitation (Swenson and Weiser, 2010) and moisture (Bjorkman et al., 2018a) on the distribution of particular plant traits (e.g., height) is well documented, thus these climate variables could also play a role in determining multi-trait diversity within the tundra biome. The dominance of particular functional groups (e.g., shrub, graminoid, forb) composition within a community can alter its trait composition (Chapin et al., 1996; Lavorel and Garnier, 2002; McGill et al., 2006). Whilst some analyses suggest only weak relationships between functional group and trait composition in tundra (Bret-Harte et al., 2008; Cornelissen et al., 2004; Hollister et al., 2005; Hudson et al., 2011; Little et al., 2015; Shaver et al., 2001; Thomas et al., 2018), the links between functional group composition and functional diversity per se are not clear.

As tundra plant composition changes in response to anthropogenic climate change, functional diversity could also shift. Shrub expansion and increases in vegetation productivity and cover indicate that functional shifts throughout the tundra biome may be underway (Berner et al., 2020; García Criado et al., 2020; Myers-Smith et al., 2020; Myers-Smith and Hik, 2017). Community-weighted traits are shifting, favouring taller plants with larger leaves and faster resource acquisition strategies (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2020). García Criado et al. (2025b) have also reported that species turnover was common throughout the tundra, yet with no net directional change in species richness across sites, mirroring trends in richness observed at global scales (Blowes et al., 2019; Dornelas et al., 2014). However, change in biodiversity can lag behind warming in the tundra (Freitag Kramer et al., 2025; Stewart et al., 2016) such that directional diversity changes and accompanying functional shifts might manifest in the future, even if the global trend of climate warming was halted. A biome-wide functional diversity shift would likely influence the stability and resilience of communities, potentially modifying global-scale feedbacks between vegetation and climate (Bjorkman et al., 2018a, 2020; Callaghan et al., 2011; Helfenstein et al., 2025; Niittynen et al., 2020; Pearson et al., 2013). Thus, understanding changes in tundra functional diversity over time will facilitate the detection of climate feedbacks in a rapidly warming tundra biome.

Here, we use *in situ* vegetation surveys and resurveys from 2,087 plots, 352 vascular plant species and 45 sites to characterise spatial and temporal patterns in functional diversity across the tundra biome. We investigated two main sets of research questions (RQs):

RQ1: How is functional diversity distributed across the tundra biome?

We predicted that with both increasing latitude (**H1a**) and decreasing ambient temperature (**H1b**), functional richness and functional dispersion would decrease alongside species richness whilst functional evenness would increase. This would hence mirror patterns seen in tree species (Lamanna et al., 2014), terrestrial birds (Schumm et al., 2019), reef fish (Halpern and Floeter, 2008) and marine bivalves (Edie et al., 2018), throughout tropical and temperate biomes globally. While temperature on average decreases at higher latitudes, additional factors such as elevation and aspect can alter the latitudinal gradient in temperature. Latitude also encompasses gradients in light conditions and biogeographic drivers, such as proximity to the boreal ecoregion. Since we could not fully separate the roles of temperature and latitude due to the collinearity between the two, we ran separate models for each, while acknowledging they cover similar, but not identical gradients. We expected to find higher functional richness, dispersion and evenness in wetter, moister locations which provide more benign areas for growth (**H1c**; Currie et al., 2004; Grace et al., 2011; Spasojevic et al., 2014; Whittaker, 1960) and are known to be major determinants of tundra plant trait distributions (Bjorkman et al., 2018a). We expected that functional diversity could differ between biogeographic regions of the Arctic due to their divergent glacial histories (Elphinstone et al., 2024) and resulting proportion of the pan-Arctic species pool (PAF, 2018; H1d; Figure 1).

Despite the assumed similarity in ecological function between species belonging to the same functional group (e.g., Lavorel and Garnier, 2002; McGill et al., 2006), studies indicate that tundra species are highly individualistic such that traditional functional groups explain only limited variation in trait composition (e.g., Bret-Harte et al., 2008; Cornelissen et al., 2004; Hollister et al., 2005; Hudson et al., 2011; Little et al., 2015; Shaver et al., 2001; Thomas et al., 2018). Therefore, we expected functional diversity to be decoupled from functional group composition (**H1e**).

RQ2: How is tundra functional diversity changing over time?

While plant height is increasing in a warming tundra (e.g. Elmendorf et al., 2015, 2012; Myers-Smith et al., 2019; Niittynen et al., 2020; Thomas et al., 2020), other traits and species richness have remained relatively stable (Bjorkman et al., 2018a; Duveneck and Scheller, 2015; García Criado et al., 2025b; Stewart et al., 2016). We therefore expected to see little temporal change in functional diversity over time (**H2a**). However, we expected that warming temperatures could lead to increases in functional diversity over time, mimicking expectations for broad-scale spatial relationships between functional diversity and temperature (**H2b**). Finally, given expected decoupling between functional diversity and functional group composition, we did not expect changes in the dominance of certain functional groups to be reflected in changes in functional diversity (**H2c**).

2 Materials & Methods

2.1 Plant composition data

Plant composition and abundance data were sourced from the International Tundra Experiment (ITEX+) dataset (Bjorkman et al., In prep.; Henry et al., 2022), an *in situ*, plot-based dataset of plant composition records spanning the tundra biome. The dataset has an inherent spatial hierarchy, with ‘plots’ representing the smallest spatial unit within this setup. Multiple plots are nested within ‘subsites’, typically a cluster of plots grouped by spatial or habitat commonalities within a wider ‘study area’, which represent the largest spatial unit within the hierarchical structure. Sites generally contain multiple subsites and span areas ranging from several hundred square metres to tens of square kilometres (García Criado et al., 2025b; Prevéy et al., 2022). Plots were also grouped into larger biogeographic regions (see **RQ1**; **Figure 1a,b**; Abbott and Brochmann, 2003; Ray and Adams, 2001; Zhang et al., 2023). Western North America contained the highest proportion of plots at 35.6%, with Greenland-Iceland comprising 32.0%, Eurasia 26.4% and Eastern North America 9.0%.

We filtered the ITEX+ dataset, predominantly following the workflow of García Criado et al. (2025b), to suit the needs of this study. Plots were retained based on both geographical and methodological criteria. Geographically, only Arctic and subarctic plots above 60° N latitude were retained. Whilst Oroarctic plots were retained, Northern hemisphere alpine plots below 60° N were removed due to the different scales over which ecological change occurs in alpine settings. Low latitude alpine sites were extremely infrequent in the ITEX+ database. This, coupled with their notably lower latitudes, would have resulted in outsized leverage of a few southern sites in the analyses, hence we removed these plots prior to analysis and focus here only on the Arctic tundra. While experiments were implemented at some ITEX+ sites, we retained only non-manipulated, ambient control plots in this study. Furthermore, only plots with consistent size between years of 1 m^2 or less were retained (mean plot size: 0.59 m^2, range: 0.048 – 1 m^2; 95.7% plots retained). This is due to the known increase in plant species richness with plot size as per the species-area relationship (Zhang et al., 2023). While we acknowledge that nonvascular plants can make substantial contributions to ecosystem function, they were not consistently identified to the species level, and were not included in this analysis. Additionally, we removed plots where vascular taxa were not all identified to the genus or species level. We included only plots where abundance was quantified as percent cover or a metric that could be converted to percent cover (e.g., Braun-Blanquet cover classes, point-framing or percent cover itself). To homogenise data from disparate sampling methods, the abundance of each vascular species in each plot was converted to relative cover (0 – 100%) of vascular plant material per plot. The relative cover per plot of three functional groups (shrubs, graminoids and forbs) was calculated by summing the relative cover values of all the species in each functional group within each plot (totalling 100%). Whilst trait differentiation within and between these groups exists (Thomas *et al*., 2020), on an aggregate level the groups show distinct responses to climate warming (e.g. Walker *et al*., 2006; Elmendorf *et al*., 2012a; 2012b).

Our final dataset comprised 45,217 plant composition records of 352 individually identified vascular plant species within 143 genera and 42 families. Quality control was undertaken following the methods of Bjorkman et al. (2018a) and García Criado et al. (2025b), including the standardisation of species taxonomy using The Plant List (TPL, 2023) within the R package 'Taxonstand' (version 2.4; Taxonstand, 2023). This dataset was used to assess patterns in functional diversity across both space (**RQ1**) and time (**RQ2**). For spatial analyses (**RQ1**), we used the latest vegetation survey of each plot only. This resulted in a dataset comprising 2,087 individual plots across 154 subsites and 45 sites throughout the Arctic and subarctic tundra (above 60 °N latitude) and spanning a period of 34 years (1988 – 2022). The mean number of plots per subsite and site were 14 and 46, respectively (**Figure 1a**).

For temporal analyses (**RQ2**), we retained only plots that had been surveyed at least twice over a period of at least five years, since diversity trends can be difficult to detect over short time scales (Valdez et al., 2023). In addition to the longer-term trends we were interested in, random interannual fluctuations in species presence, and therefore functional composition, certainly occur in these perennial plant communities (Harris et al., 2022; Valdez et al., 2023) and detection of species is not entirely complete using point framing methods (May and Hollister, 2012). We acknowledge that shorter time-series, and those with fewer survey points, may show more variable trends but should not be biased towards increasing or decreasing functional diversity. We therefore included all plots with at least two survey points at least five years apart in our temporal analyses in order to maximize the broad spatial representation of our analyses (**Figure 1a,b; S1**). Non-permanently marked ITEX plots were not used in the temporal studies due to the uncertainty introduced by relocation between years. The first instance of each plot was used in the spatial dataset where relocation was not an issue. This filtering yielded a final dataset of 1,188 individual plots across 86 subsites and 22 sites for the temporal analysis. The temporal dataset spanned a period of 38 years (1984 – 2022) with a median monitoring duration of 12 years (range: 5 to 28 yrs) and a mean of 3.8 time points per plot (range: 2 to 9 surveys per plot).

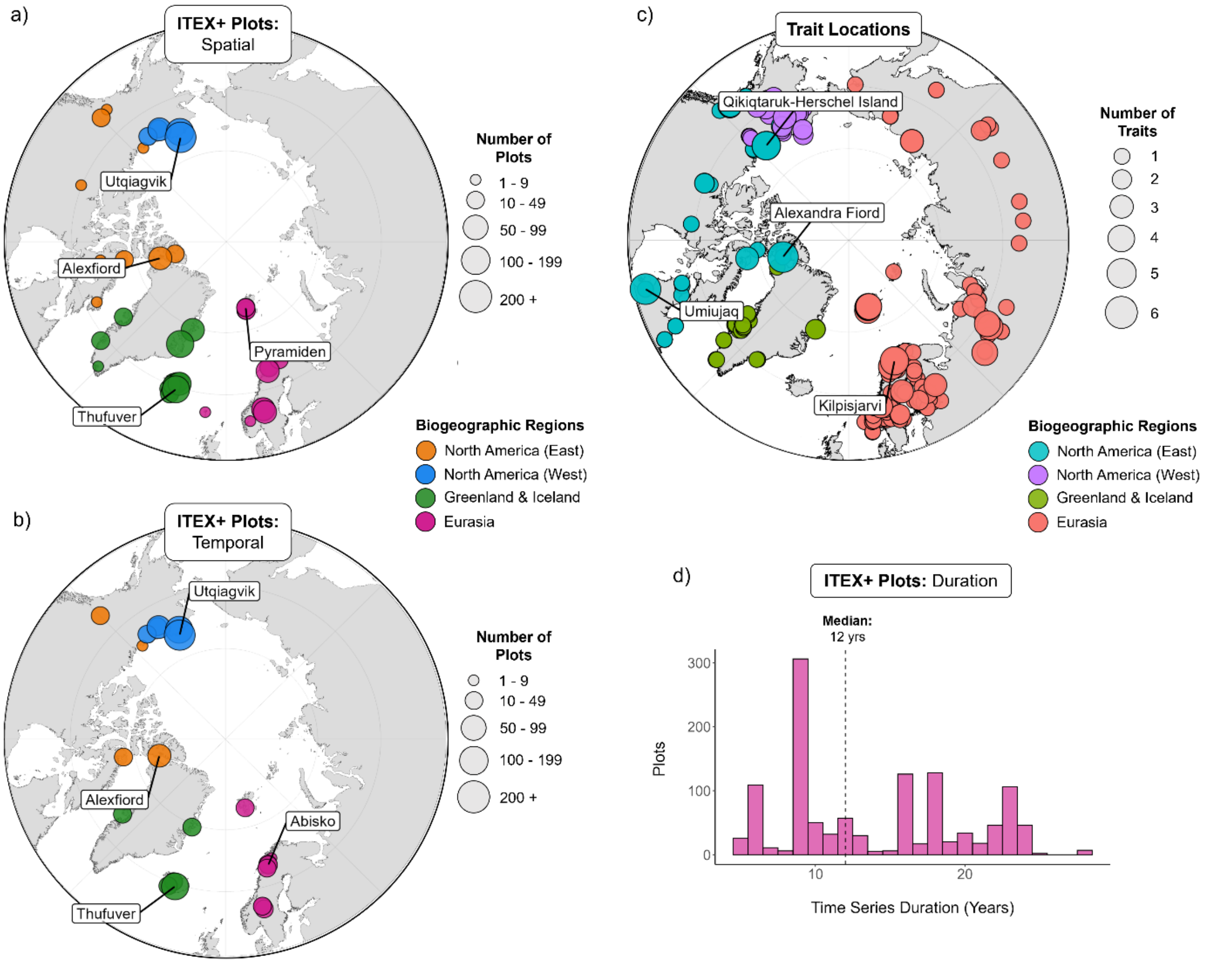

Figure 1. Geographical distribution of our plot-survey data. Distribution of the **a)** 45 spatial sites, and **b)** subset 22 temporal sites, from which composition data from the ITEX+ dataset was incorporated. Sites are coloured by biogeographic region and circle size indicates the number of ITEX+ plots analyzed from within that site (ranging from one plot in Kluane, YT, Canada to 302 in Utqiagvik, AK, USA). Selected sites with labels are typically those with the largest number of sampled plots in that region. The 45 sites spanned a latitudinal gradient of 20.78°. **c)** Distribution of the 133 locations from which Tundra Trait Team (TTT) (108 locations) and TRY (25 locations) trait data were drawn. Circle size indicates the number of continuous traits sampled at that location (ranging from one trait at 72 locations to six traits at two locations, out of a maximum of seven). Sites containing the highest number of sampled traits were labelled. All maps have a polar projection with a southern latitudinal limit of 55° N. **d)** Duration (years) of the time series of the 1,188 plots that comprise the temporal ITEX+ dataset (minimum duration = five years).

2.2 Climate data

Climate data was sourced for the period 1979 to 2013 from CHELSA climatologies (version 1.2.1; Karger et al., 2017), given its fine spatial resolution (1 km × 1 km) and demonstrated accuracy, particularly for precipitation (Datta et al., 2020; Karger et al., 2017; Maria and Udo, 2017). While the exact dates of vegetation sampling varied among sites, we opted to use a consistent time window for climate data that had high temporal overlap with the plant composition dataset. This approach is consistent with other recent analyses (García Criado et al., 2025b). Because tundra plants are perennial, grow slowly and vegetation change lags behind climate, climate from previous years should still be influencing vegetation change for a number of subsequent years. Climatological variables were extracted for each subsite within the ITEX+ dataset. We extracted the long-term average values for mean and maximum warmest quarter temperature (WQT), mean and minimum coldest quarter temperature (CQT), and mean annual precipitation (hereafter, precipitation) from the climatologies. The four temperature variables were all highly correlated. As such, following García Criado et al. (2025b), we proceeded with mean WQT (hereafter just "temperature") as our sole temperature variable due to well-documented impacts of summer warming on tundra vegetation (Rayback and Henry, 2005; Van Der Wal and Stien, 2014; Weijers et al., 2010). A categorical soil moisture variable - dry, moist, or wet - was also extracted from the ITEX+ dataset for each plot (hereafter just "moisture"). Additionally, time series of the mean air temperature throughout the warmest quarter (June – August) and annual precipitation were extracted for each subsite for each year from 1979 and 2013. Change over time in temperature and precipitation were calculated by fitting linear models of yearly climatic values over this time period, and using the slopes of change per plot as fixed effects in the multivariate models, as outlined in detail in **Section 2.6**.

2.3 Trait data

For our functional diversity analyses, we selected traits that: (1) have been considered influential to tundra ecosystem functioning (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2020, 2018); (2) contribute strongly to one of the two main axes in plant trait variation, the leaf economic spectrum (LES) and size (see **Table S1**; Thomas et al., 2020); and (3) were relatively well-represented in plant trait databases (see below). Seven continuous, above-ground plant functional traits were selected: leaf dry matter content (LDMC; g g^{-1}); leaf area (mm^2); leaf nitrogen concentration (leaf N; mg g^{-1}); leaf phosphorus concentration (leaf P; mg g^{-1}); plant height (hereafter, height; m); seed dry mass (SDM; mg); and specific leaf area (SLA; mm^2 mg^{-1}). Two binary traits, evergreenness and woodiness (yes = 1 and no = 0 in both cases), as derived from the functional group classification of each species (forb, graminoid and deciduous or evergreen shrub), were also included. For more information on the selection of the nine functional traits and their considered relevance to tundra ecosystem functioning, see **Table S1**.

Data for the seven continuous traits were extracted from two global databases of plant traits: the TRY plant trait database (version 5; Kattge et al., 2020) and the Tundra Trait Team (TTT) database (version 1; Bjorkman et al., 2018b). All Northern Hemisphere records from the TTT database were retained as they were sampled from known tundra locations (including alpine plots), thereby reducing gap-filling requirements and maximising the use of available high quality data. In the TRY database, however, only records from above 60° N were retained to align with the criteria used for the inclusion of plant composition data and uncertainty about whether lower-latitude collections were from alpine tundra regions. In addition to extracting trait measurements for species identified in our sample plots, we also extracted trait measurements for any species that was collected within the target geographic range for use in trait gap-filling (see **Section 2.4**). The majority of final trait values were sourced from the TTT database (47,499 individual records) with a smaller number of trait measurements included from TRY (5,035 records), leading to a combined total of 52,534 unique records across the seven continuous traits. The respective proportions of this total contributed by each trait were: height (36.1%; 18,955 records); SLA (18.6%; 9,789 records); leaf area (16.9%; 8,857 records); LDMC (13.1%; 6,857 records); leaf N (10.0%, 5,235 records); leaf P (3.4%; 1,773 records); and SDM (2.0%, 1,068 records).

Quality control was undertaken following the methods of Bjorkman et al. (2018a), García Criado et al. (2025b) and the ITEX+ dataset, including the standardisation of species taxonomy using The Plant List (TPL, 2023) within the R package ‘Taxonstand’ (version 2.4; Taxonstand, 2023). Records were also sorted into biogeographic regions for gap-filling (**Figure 1b**). Both automated and manual error checking was also incorporated during the production of the final dataset to ensure the accuracy of the retained records. Error checking included, but was not limited to, the identification of duplicate records, removal of significant outliers and erroneous data values and standardisation of accepted vegetative and reproductive height records. For full details on the automated and manual error checking, see **Supplementary Method S1**.

2.4 Gap-filling

A prerequisite to calculation of functional diversity indices is data for all traits for each species occurring in each vegetation plot. However, traits were rarely measured in the exact same sites as species composition, and some species-trait combinations were missing altogether. We therefore created a two-step hierarchical gap-filling algorithm that aims to infer missing trait values preferentially from nearby locations and taxonomically close relatives. For full details on the automated and manual error checking, see **Figure S2** and **Supplementary Method S2**.

2.5 Functional diversity metrics

No single functional diversity index can capture the nuances and complexities of functional diversity alone (Villéger et al., 2008), hence we analysed three key metrics of functional diversity in this study: (1) functional richness; (2) functional evenness; and (3) functional dispersion. Functional richness quantifies the volume of the multi-dimensional trait space occupied by a community of species, a multivariate analogue of range. Functional evenness quantifies the distribution of species within the multivariate trait space (Laliberté and Legendre, 2010; Villéger et al., 2008). Functional dispersion, or the abundance-weighted mean absolute distance of all species to the centroid, describes the variability of species traits in a community in a way that is mathematically independent of species richness, which provides an important additional axis of potential change (de Arruda Almeida et al., 2018; Laliberté and Legendre, 2010). To help conceptualise how functional richness, evenness and dispersion vary in response to different types of biodiversity change (e.g., changes in species richness, trait values and relative abundance), please see the simulated data in **Figure S3**.

The effects of changing one or more aspects of functional diversity on ecosystem function is an active area of research (e.g. Clark et al., 2012; Gagic et al., 2015; Wen et al., 2019) with little consensus yet as to how changing individual aspects of functional diversity (e.g. richness vs. evenness) affects ecosystem services. That said, we know that maintaining functional richness is most important where rare species provide unique ecosystem functions (Jain et al., 2014), whereas conserving functional evenness prioritises communities where unique functions are not limited to a few (potentially vulnerable) species, increasing the potential for complementarity and optimal resource use (Mouillot et al., 2005, and references therein). Functional dispersion was included to capture aspects of functional diversity that are not confounded with changes in species richness. We included it for this reason but note that its effects on measured ecosystem function are less well studied than those of functional richness and evenness. All three indices are used widely in the literature and capture different yet complementary aspects of community functional diversity, hence providing a more complete understanding (Hejda and Bello, 2013; Laughlin et al., 2017; Lozanovska et al., 2020; Niittynen et al., 2020; Yang et al., 2017).

We used the 'FD' package in R to calculate functional diversity indices (version 1,0-12.3; Laliberté et al., 2023). This package employs a distance-based framework and is highly flexible, accepting any number or type of traits whilst also weighting individual traits by the relative abundance of the constituent species (Laliberté and Legendre, 2010). Using the 'dbFD' function, we calculated functional richness, functional evenness and species richness across the 2,087 spatial and 1,188 temporal plots. The convex-hull volume approach used by this function requires at least three species to compute functional evenness and four species to compute functional richness. Functional richness and evenness were therefore undefined for plots with species richness < 4 and < 3; respectively, resulting in slightly different sample sizes in the final analyses, depending on the functional diversity metric used. Final sample sizes were 1,822 plots for functional richness models, 1,950 plots for functional evenness and 2,087 plots for functional dispersion in the spatial analyses, and 1,053 plots for functional richness models, 1,131 plots for functional evenness and 1,164 plots for functional dispersion in the temporal analyses.

The initial step in calculating functional richness is to reduce the dimensionality of the given trait data to a number of effective traits (numT). The numT used can impact the value obtained when functional richness is calculated and hence must be carefully considered (Carvalho and Cardoso, 2020; Laughlin, 2014; Legras et al., 2020; Mammola et al., 2021; Zihao et al., 2021). In plant communities, the addition of more traits, up to a point, is considered to lead to a better ability to predict functional composition (Laughlin, 2014). However, the numT selected must also be less than the number of species for functional richness to be defined, leading to a trade-off between inclusion of more traits or inclusion of species-poor plots. The addition of too many traits, however, can reduce the reliability of computed functional richness due to insufficient trait observations to support their inclusion (Bellman, 1966; Mammola et al., 2021). Using the numT = 3 parameterisation, functional richness is defined for all plots with four or more species (87.3% and 92.5% of plots in the spatial and temporal datasets respectively).

2.6 Statistical analyses

Two main groups of statistical models were used in this study: (1) one group based on spatial comparisons (RQ1), and (2) another group based on temporal comparisons (RQ2). Where possible, we aligned our statistical methods with those of García Criado et al. (2025b) in order to directly compare changes in functional diversity to changes in taxonomic diversity across the same region. All models run with functional diversity response variables were also run with species richness as a response variable to facilitate comparisons between functional and species richness responses using an identical dataset. The species richness results align with those of García Criado et al. (2025b), who used a slightly smaller but largely overlapping dataset, and are presented in the Supplementary Materials. For full details of model structures, see **Table S2**. Unless stated otherwise, all statistical analyses were run in the R programming language (version 4.2.0; R Core Team, 2022). Models were run in a Bayesian framework within 'brms' (Bürkner et al., 2023), an R package with a 'Stan' backend (Stan Development Team, 2024). Models were run for as many iterations as necessary in order to achieve convergence (minimum 2000 iterations, 500 warm-up), as assessed by trace plots and corresponding R_{hat} scores. In rare instances, the explanatory variable was centred, but not standardised (and outputs back-transformed), to aid convergence.

2.6.1 Spatial comparisons

To assess latitudinal gradients in functional diversity, we fitted four distinct Bayesian mixed-effects models with: (1) functional richness; (2) functional evenness; (3) functional dispersion and (4) species richness as response variables. Natural log-transformed plot size was included as a covariate in all models to account for variable plot sizes (Drakare et al., 2006; Rosenzweig, 1995). Models incorporated a nested random intercept of subsite (45 levels), nested within 0.5 x 0.5 degree latitudinal/longitudinal grid cells, to account for both the nested sampling structure and the close proximity of multiple sites in certain regions of the tundra (e.g. Iceland; **Table S2**).

We also ran a second set of four models with biogeographic region (factor variable; four levels; **Figure 1**) replacing latitude as a fixed effect to determine whether functional diversity differed systematically between tundra regions.

We incorporated species poor plots (those with three or fewer species, for which functional richness is not defined) by using censored models, rather than excluding these plots. In these models, the functional richness of such plots was entered as a censored variable with a value between zero and the median observed functional richness of plots with four species. Whilst functional richness displayed a lognormal distribution, the model would not converge using this distribution within a censored model structure. We therefore ran the model using a Gaussian distribution and a log-transformed functional richness variable. We used a negative binomial distribution for species richness, and a Gaussian distribution for models of both functional evenness and functional dispersion (for details, see **Table S2**).

To identify potential abiotic factors related to functional diversity, we tested the relationship between temperature, precipitation, moisture and our four diversity metrics. To understand how diversity changes with the dominance of particular functional groups, we ran a second set of models with shrub cover, forb cover and graminoid cover (all continuous) as explanatory variables. As we expected functional and species diversity to be greatest where no functional group dominated the composition, the models with shrub, forb and graminoid cover as fixed effects included both a linear and quadratic functional group cover term (**Table S2**). All models included the natural log-transformation of plot size and the same random effects structure as outlined in the latitude models above.

Last, to illustrate the relationships between functional diversity and species richness in the tundra, we fitted three independent general additive models (GAMs) in R using the ‘mgcv’ package (Wood, 2023) with: (1) functional richness; (2) functional evenness; and (3) functional dispersion as the respective response variables and species richness as the only predictor variable (**Table S2**). These were intended as descriptive models purely to illustrate the relationships between each metric in our dataset, and not as a statistical comparison to test our a priori hypotheses.

2.6.2 Temporal comparisons

To assess change over time in functional diversity, and key variables including temperature and functional group cover (**RQ2**), we first calculated the rate of change per plot in each as the slope of a linear model between each variable and sampling year. For these analyses, we restricted our dataset to the 1,188 plots that had been sampled at least twice over a five year period, estimating plot-level rates of changes in the following response variables: functional richness, evenness, dispersion, and species richness. To identify key variables related to diversity change over time, we tested relationships between latitude, temperature, temperature and precipitation change (measured at the subsite level), and shrub, forb and graminoid cover change (measured at the plot level) and the four diversity metrics. As with the spatial analyses, each variable was used as a fixed effect in separate mixed-effect models.

As above, all models included natural log-transformed plot size as a fixed effect and random effects of subsite nested within biogeographic region. All temporal change models were run using a Gaussian response distribution with an identity link function (**Table S2**). While inverse-variance weighting is commonly used in two-step analyses such as ours (Hedges and Olkin, 2014), some of our plots had only two sampling points, which meant that the standard-error on the slope (rate of change) was not always estimable. Consequently, we did not weight plots by the standard-error of the slopes as is often done when the response variable is measured with uncertainty.

3 Results

3.1 Functional diversity across space

Across the tundra biome, we found that functional richness notably declined in tandem with increasing latitude (**Figure 2a**; CIs: -0.0656 to -0.0017). Functional evenness displayed a contrasting trend, instead increasing moderately with latitude, although the confidence intervals for this relationship overlapped zero (**Figure 2b**; CIs: -0.0004 to 0.0088). Functional dispersion exhibited no relationship with latitude (**Figure 2c**). Mirroring the patterns seen with latitude, functional richness showed positive relationships with temperature (**Figure 2d**; CIs: 0.0144 to 0.1192) whilst functional evenness showed a negative relationship with temperature (**Figure 2e**;

CIs: -0.0205 to -0.0074). Functional dispersion again exhibited no notable relationship (**Figure 2f**). Patterns in functional richness, mirrored those seen in species richness across the biome (García Criado et al., 2025b; **Figure S4**; **S5**). None of functional richness, evenness or dispersion exhibited strong relationships with precipitation (**Figure S5**) or soil moisture (**Figure S7**) across the tundra. Furthermore, neither functional richness nor dispersion differed among biogeographic regions, although functional evenness was higher across both North American regions when compared to Eurasia (**Figure S8**). Finally, all of functional richness, evenness and dispersion were maximized at intermediate levels of cover for all functional groups (with the exception of functional evenness and forbs; CIs: Forbs = -0.00004 to 0.00000), declining as cover of any single functional group approached either extreme (0 or 100%; **Figure 2g-i**; **Table S2** for full CIs).

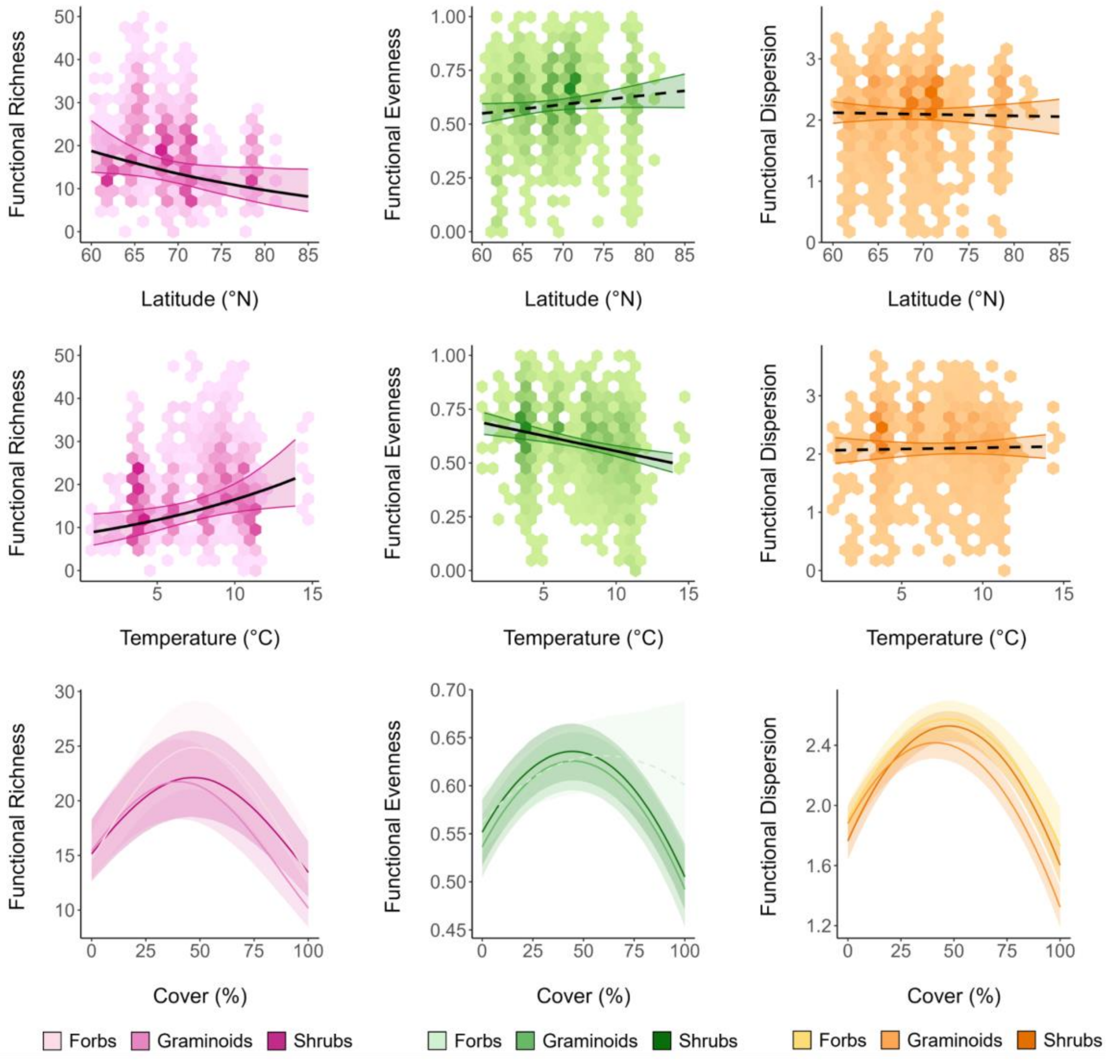

Figure 2. Functional diversity followed expected patterns in latitude and temperature across the tundra biome and was maximised when cover was evenly distributed between functional groups. Relationships between latitude and **a)** functional richness (*n* = 1,822), **b)** functional evenness (*n* = 1,950), and **c)** functional dispersion (*n* = 2,087), and temperature and **d)** functional richness (*n* = 1,822), **e)** functional evenness (*n* = 1,950), and **f)** functional dispersion (*n* = 2,087). For plots **a-f)**, lines and ribbons are drawn from the model outputs in **Table S2** (solid line = 95% CIs do not overlap zero; dashed line = 95% CIs overlap zero). Hexbin colours represent the number of plots within each bin. Relationships between forb, shrub and graminoid cover, and **g)** functional richness (*n* = 1,822), **h)** functional evenness (*n* = 1,950), and **i)** functional dispersion (*n* = 2,087). Disaggregated versions of plots **g-i)**, including the plot-scale data behind the curves, can be found in **Figure S9**. For plots **g-i)**, the lines and ribbons are drawn from the model outputs in**Table S2**. CIs represent the 95% CIs on the quadratic term of the model outputs in **Table S2** (solid line = 95% CIs do not overlap zero; dashed line = 95% CIs overlap zero).

3.2 Functional diversity over time

Functional richness (**Figure 3a**; CIs: -0.1024 to 0.0749), functional evenness (**Figure 3b**; CIs: -0.0030 to 0.0013) and functional dispersion (**Figure 3c**; CIs: -0.0062 to 0.0095) remained relatively stable over time. Some individual plots showed increases or decreases in functional richness, evenness or dispersion, but the mean change was centred on zero, with an approximately even balance of both increases and decreases across plots within our dataset (**Figure 3a-c**). Changes in functional richness, functional evenness and species richness over time were also unrelated to either latitude, site temperature or precipitation (**Figure S11**; **S12**; **S13**). Changes in functional richness (**Figure 3d**; CIs: -10.8452 to 1.8692), evenness (**Figure 3e**; CIs: -0.1251 to 0.1710) or dispersion (**Figure 3f**; CIs: -3.6796 to 0.7015) were unrelated to temporal changes in temperature and precipitation (**Figure S14**).

Changes in cover and dominance of the forb, shrub and graminoid functional groups were associated with changes in functional richness, evenness, and dispersion. Specifically, we found that increases over time in forb cover were associated with increases in functional richness (**Figure 3g**; CIs: 0.0644 to 0.1106), evenness (**Figure 3h**; CIs: 0.0014 to 0.0030) and dispersion (**Figure 3i**; CIs: 0.0268 to 0.0427). Conversely, increased shrub cover led to notable reductions in functional richness (**Figure 3g**; CIs: -0.0607 to -0.0260) and dispersion (**Figure 4i**; CIs: -0.0204 to -0.0091), whilst increased graminoid cover led to reduced functional evenness (**Figure 3h**; CIs: -0.0014 to -0.0002).

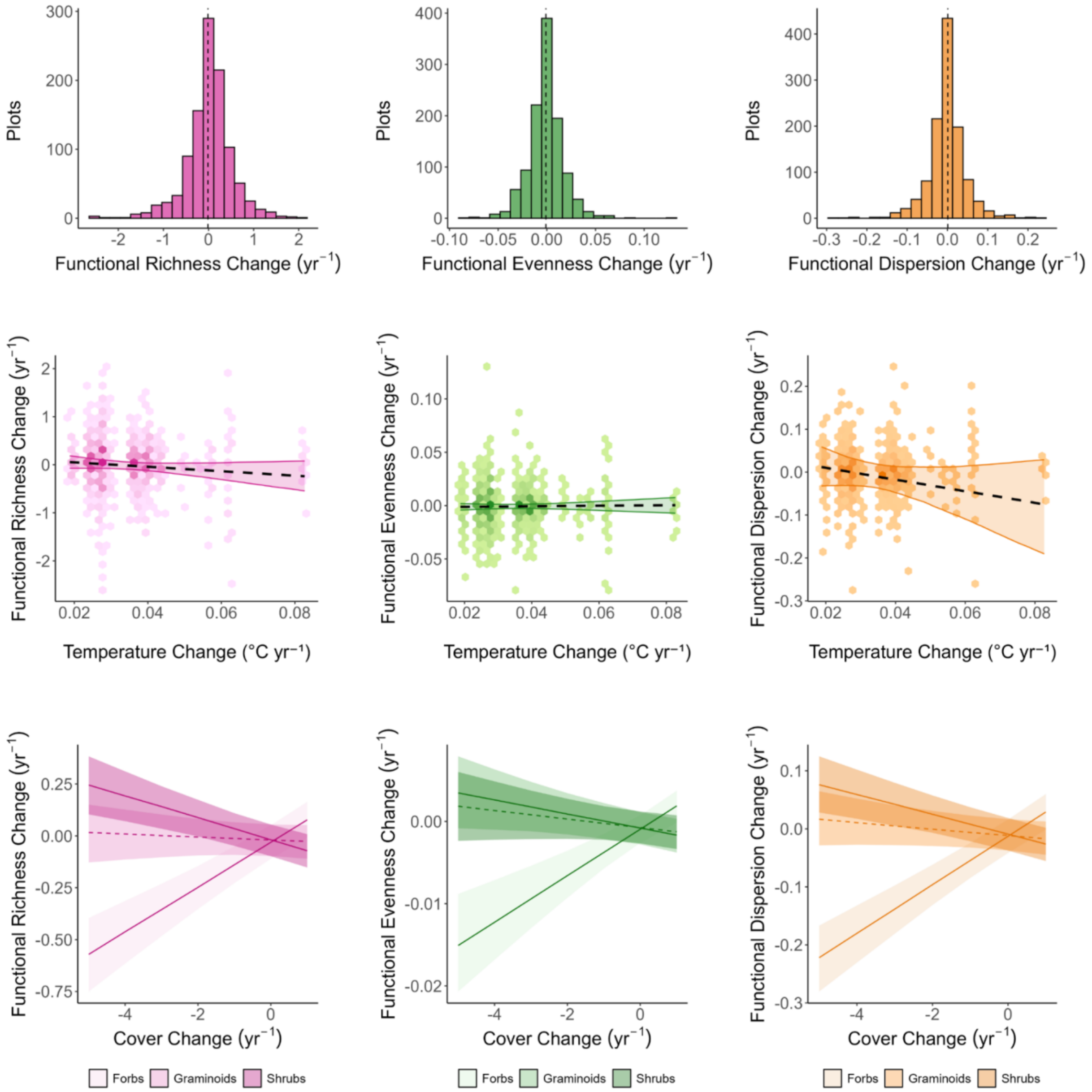

Figure 3. There was no net directional change in functional diversity across the tundra biome, although individual plot-level changes were associated with changes in functional group cover not temperature. Relationships between time and change in **a)** functional richness (*n* = 1,053), **b)** functional evenness (*n* = 1,131), and **c)** functional dispersion (*n* = 1,164), and temperature change and change in **d)** functional richness (*n* = 1,053), **e)** functional evenness (*n* = 1,131), and **f)** functional dispersion (*n* = 1,164). For plots **a-c)**, change in all three indices was calculated for all plots surveyed at least twice over a period of at least five years with 95% CIs drawn from the model outputs in **Table S2**. For plots **d-f)**, hexbin colours represent the number of plots within each bin and lines and ribbons are also drawn from the model outputs in **Table S2** (solid line = 95%

CIs do not overlap zero; dashed line = 95% CIs overlap zero). Relationships between change in forb, shrub and graminoid cover, and change in **g)** functional richness (*n* = 1,053), **h)** functional evenness (*n* = 1,131), and **i)** functional dispersion (*n* = 1,164). For plots **d-i)**, all confidence intervals represent the 95% confidence interval on the slope estimate of temperature or cover change over time with all lines, ribbons and CIs drawn from model outputs in **Table S2** (solid line = 95% CIs do not overlap zero; dashed line = 95% CIs overlap zero).

4 Discussion

We found that throughout the tundra biome, functional richness was higher in warmer, lower latitude locations, whilst functional evenness was maximised in cooler, more northerly tundra regions (**Figure 2a-f**). All three metrics of functional diversity were maximised when cover was evenly distributed between functional groups (**Figure 2g-i**). Furthermore, whilst we found no net directional change in functional richness, evenness or dispersion over time (**Figure 3a-c**), plot-scale changes in functional diversity were correlated with change in functional group cover over time (**Figure 3g-i**), but not change in temperature (**Figure 3d-f**). Increased forb cover led to increases in all measured facets of functional diversity whilst increased shrub cover led to corresponding declines in functional richness and dispersion (**Figure 3g-i**). Our results highlight the potential consequences of changes in tundra species composition, such as shrubification (García Criado et al., 2020; Myers-Smith et al., 2011; Myers-Smith and Hik, 2017), for ecosystem functioning over the coming decades.

4.1 Reduced functional diversity in the highest latitude and coldest regions

Consistent with our predictions, we found evidence for higher functional richness and lower functional evenness in lower latitude (**H1a**), warmer (**H1b**) locations. Indeed, relationships between functional richness and particularly evenness, and temperature were stronger than those with latitude (**Figure 2a-f**), likely due to the influence of local and regional variability, such as microclimate, altitude and continentality, that weakens global latitude-temperature relationships. These patterns mirror the latitudinal and temperature gradients seen in species richness across the tundra (García Criado et al., 2025b; **Figure S4**) and reflect patterns seen throughout other biomes globally. The monotonic decline in functional richness alongside the latitudinal gradient species richness has been documented across temperate and tropical regions (Edie et al., 2018; Halpern and Floeter, 2008; Lamanna et al., 2014; Schumm et al., 2019) and our work supports the continuation of this gradient throughout the tundra biome.

Studies in taxa ranging from bats, to marine bivalves to woody plants (Edie et al., 2018; Stevens et al., 2003; Swenson et al., 2012) have found decreases in functional richness towards higher, colder latitudes due to a progressive loss of species and corresponding traits. More environmentally favourable conditions at warmer, lower latitudes however, typically support species from more diverse functional strategies and enable greater niche specialisation, thereby increasing both species and functional richness (Edie et al., 2018; Pastore et al., 2021). The benign conditions however, allow many additional species to establish in already occupied niches, leading to oversaturation in certain portions of trait space and little in terms of new trait variation. As such, species richness may increase at a greater rate than functional diversity, leading to a decoupling of species and functional diversity and – in some cases – surprising hotspots of functional diversity outside of the tropics (Oliveira et al., 2016; Stuart-Smith et al., 2013). This oversaturation instead drives reduced functional evenness and increased functional redundancy (Halpern and Floeter, 2008; Schumm et al., 2019). Both the decrease in functional richness and increase in functional evenness towards higher latitudes found in our study (**Figure 2a-f**), together with an apparent leveling-off of functional richness in our highest species richness plots (**Figure S5**), suggest that similar biogeographic relationships between species and functional diversity extend through the tundra biome to the northern high latitudes.

While patterns in functional richness followed those seen in species richness across the tundra, patterns in functional dispersion did not (**Figure S4**). Functional richness as a metric, can increase due to both increased species richness, or while holding the number of species constant but instead increasing the variability of traits (e.g. Mouchet et al., 2010; Schleuter et al., 2010). In our system, as described above, we found that gradients in functional richness largely followed those in species richness – increasing at warmer, lower latitudes. In contrast, we found functional dispersion, a functional diversity metric mathematically independent of species richness (de Arruda Almeida et al., 2018), was largely constant across major environmental gradients. Together, these results imply that the broad-scale geographic patterns in functional richness in our study system are mainly driven by the addition or removal of species. This finding is supported by the strong relationship that we observed between functional richness and species richness, and the comparatively weak relationship between functional dispersion and species richness (**Figure S5**). These results suggest that as species are lost or gained from tundra communities, functional richness, and the ensuing ecosystem services provided by a functionally diverse community, such as resistance and resilience in the face of climate extremes (Helfenstein et al., 2025), will likely change in step.

4.2 Functional change lags behind warming

In line with results for species richness (García Criado et al., 2025b), and consistent with our prediction, we found no net directional change in functional richness or evenness over time during a period of rapid warming at high latitudes (**Figure 3a-c**). We suggest three potential explanations for this lack of change: slow species turnover, mean trait shifts in the absence of changing trait diversity, and turnover amongst functionally similar species. Niche modeling suggests that northward range expansion should eventually increase functional diversity in the boreal region (Thuiller et al., 2006) and we expect migration of boreal species into the tundra would have similar effects. However, plant immigration and establishment are slow processes, particularly in tundra ecosystems dominated by long-lived perennial species (Duveneck and Scheller, 2015). As such, changes may not manifest for decades (Alexander et al., 2018), limiting the influx of new species and traits into tundra communities (Bjorkman et al., 2020; García Criado et al., 2025a). Furthermore, in a study of tropical forests, changes in mean trait values occurred in the absence of shifts in trait variability (Carreño-Rocabado et al., 2012). Hence, whilst the region of functional space occupied by a community shifted over time, the net volume, and thus functional richness, remained consistent over time. A similar phenomenon of changes in mean functional trait composition without substantial changes in functional trait diversity could be occurring in the tundra biome. Previous studies in tundra, including a synthesis of a large subset of the data analysed here (Bjorkman et al., 2018a), found that plant height is increasing as compositional turnover increasingly favours taller species with larger leaves and faster resource acquisition (Thomas et al., 2020). However, surprisingly, we find that these increases in mean trait values are not accompanied by increased trait diversity. Finally, not all changes in species composition result in changes in functional diversity. For instance, García Criado et al. (2023) found that both ‘winner’ and ‘loser’ shrub species in the tundra typically occupied similar trait spaces, thereby highlighting that turnover does not always introduce new trait variability to an ecosystem.

4.3 The importance of changing functional group dominance

Despite a lack of net change in functional diversity seen here, as well in other systems (Freitag Kramer et al., 2025), numerous individual plots exhibited both increases and decreases over time (**Figure 3a-c**). Contrary to expectations however, we found that changes in functional diversity did not correspond to the magnitude or direction of warming (**Figure 3d-f**), but instead were associated with changes in functional group cover and dominance over time (**Figure 3g-i**). Increasing forb cover was associated with increased functional richness, evenness and dispersion, whilst increased shrub cover was associated with decreased richness and dispersion and increased graminoid cover decreased evenness (**Figure 3g-i**). Past tundra vegetation analyses have suggested only weak relationships between functional group composition and trait composition (Körner et al., 2016; Little et al., 2015; Thomas et al., 2018). However, our results here emphasise that growth forms do differ in important ways in terms of the variability in functions performed in extant communities, and that changes in their respective dominance is associated with consequential impacts for functional diversity.

Shrubs and graminoids typically encompass less trait variation than forbs (Thomas et al., 2018) which could partially explain the contrasting consequences for functional richness due to increases in shrubs versus forbs. That said, whilst forb species displayed greater variation in leaf economic traits in our data, shrubs exhibited greater structural variation, suggesting that leaf economic traits may have been more influential in driving the functional richness responses seen in our study (**Table S3**). Furthermore, shrubs can dominate plots, displacing sub-canopy and less competitive species (Boscutti et al., 2018; Pajunen et al., 2012, 2011; Scharnagl et al., 2019; Walker et al., 2006; Wallace and Baltzer, 2020), whilst graminoids, being good competitors, typically exclude species-rich forb groups due to greater height and enhanced nutrient uptake from deeper-reaching roots (Bråthen et al., 2021; Klanderud et al., 2015; Liu HuiYing et al., 2018; Myers-Smith et al., 2019). When a single dominant or few co-dominant species with similar traits are able to outcompete diverse forb species, both species and – more importantly – functional richness and evenness will likely be reduced.

While shrub cover appears relatively stable over time in the ITEX+ dataset (**Figure S15**; García Criado et al., 2023, 2020) warming-induced shrub expansion has been found in many northern high latitude studies (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2020, 2011; Myers-Smith and Hik, 2017; Tape et al., 2006). Here, we found that shrub increases are accompanied by declines in tundra functional richness and dispersion, hence any future shrub expansion, as widely expected, could lead to declines in both aspects of ecosystem function. Less diverse and functionally rich and even communities often perform fewer functions and are less stable and resistant to sudden landscape-scale changes (Cui et al., 2024; Niittynen et al., 2020). Therefore, if tundra shrub expansion is widespread in the future, this could alter ecosystem functions and services across the biome, and the wildlife and people that rely on those services (Callaghan et al., 2011; Imbert et al., 2021).

4.4 Future research

Our objectives were to investigate biome-scale patterns in tundra functional diversity across both space and time. A trade-off of this approach is that our investigations were limited to including only commonly measured traits and reliably censused taxa. The contributions of root traits and non-vascular species to ecosystem function are potentially substantial, yet their current taxonomic and geographic coverage remains lower than that of above-ground vascular traits. There is an increasing availability of below-ground (Klimešová et al., 2017, 2012) and non-vascular (Lett et al., 2021; Lewis et al., 2017) plant data and we anticipate that as these datasets grow, they may be able to be incorporated in future syntheses of tundra functional diversity. We also acknowledge the high degree of trait gap-filling required for certain traits, such as Seed Dry Mass and leaf phosphorus (**Figure S2c**), although we believe our results are robust to the levels of gap-filling employed (Everest et al., 2024). Plant composition data are also becoming increasingly available from underrepresented areas of the tundra, such as Russia (**Figure 1a**; Zemlianskii et al., 2023). More comprehensive trait datasets with sampling undertaken across a greater number of years, from sites better aligned with those of the composition records, and for a wider array of traits would permit more ecologically meaningful characterization of temporal and spatial variation in functional diversity. Finally, the continued development of tools beyond plot-based *in situ* surveys, such as hyperspectral imaging, may facilitate higher spatial and temporal resolution assessments of large-scale patterns in tundra functional diversity in the future (e.g. Beccari et al., 2023; Schneider et al., 2017; Schweiger et al., 2018).

Future studies may also benefit from further consideration of factors that may have influenced our ability to detect net, directional change in functional diversity over time. One such limitation is the relatively short average survey duration at each site (~14 years). Given the typically slow, lagged nature of change in high latitude plant communities (Duveneck and Scheller, 2015), change happening over longer time scales may not have been apparent in the comparatively short period between surveys and resurveys. Furthermore, mismatches in spatial scales between vegetation plots (1 m^2) and climate data (1 km^2) may be preventing the detection of fine-grained, climate-driven changes in functional diversity. Additional studies that benefit from longer time series paired with microclimate temperature sensors may be able to detect temporal changes in diversity beyond those found in these analyses. Finally, further studies may consider the influence of additional potential drivers of functional diversity change. These could include microclimate, known to influence key intraspecific trait variation in Arctic and alpine vegetation (Kemppinen and Niittynen, 2022), herbivory, where pressures are known to alter rates of tundra diversity decline (Olofsson and Post, 2018; Post et al., 2023, 2021), and the indirect effects of changes in climate, such as snow cover duration (Niittynen et al., 2020). Incorporating these factors into future analyses will enhance our understanding of how and why functional diversity is changing throughout the tundra.

5 Conclusions

We show that biome-scale spatial patterns in tundra functional diversity follow temperature and latitudinal gradients, but temporal changes in functional diversity tracked only the local expansion of particular growth forms, rather than abiotic drivers. The biogeographic patterns that we found in tundra functional diversity extend known global latitudinal gradients in functional diversity (Edie et al., 2018; Halpern and Floeter, 2008; Oliveira et al., 2016; Schumm et al., 2019) to the far northern reaches of our planet. While we did not find a net directional shift in tundra functional diversity, plot-scale increases and decreases both occurred. Against expectations, we found that changes in functional diversity were not associated with the magnitude of warming, but instead the changing cover and dominance of functional groups. Increasing forb and decreasing shrub and graminoid cover led to increased functional richness, evenness and dispersion. As a result, expected widespread increases in tundra shrub cover (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011; Myers-Smith and Hik, 2017) could drive declines in functional richness across the biome. Such future losses in functional diversity have the potential to influence and perpetuate cascading impacts on ecosystem functions, processes and consequently services throughout the tundra.

Data and code availability statement:

Code/data for this project archived in the following Zenodo repository: https://zenodo.org/records/17617000?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjJiNTNmYzU0LTg0NTgtNDAwZi1hNGUxLTE4Y2E1ZjMzNmY4MSIsImRhdGEiOnt9LCJyYW5kb20iOiI4OWM5NjY1OWNiZmI0ZTdlMmQ1ZmI5ZTUwN2ZiM2VhMiJ9.uxmkCWPt0IEz3yErWyGFJkgPlh6jWQac-Ubu9GmcQG4I4ESUTWRwf3-3wyYQXdwmFKn6LKZzdBcY1Eq467GUDA. The TTT trait data can be found at: https://github.com/TundraTraitTeam/TraitHub, TRY trait data at: https://www.try-db.org/TryWeb/dp.php and CHELSA climate data at: https://chelsa-climate.org/downloads/.

Acknowledgements:

We thank those who have helped compile the ITEX+ dataset, including Zoe Panchen, Antoine Becker-Scarpitta, Janet Prevéy, Jonathan Von Oppen, Karin Johansson and Jonathan J. Henn. We are particularly grateful to all local and indigenous communities for the opportunity to work with data collected from their lands. JJE was funded by a NERC E4 DTP studentship. SCE acknowledged funding from NSF-OPP 1836839. SCE and MJS were supported by the NSF-funded Niwot Ridge LTER program (NSF DEB – 1637686, NSF DEB-2224439). SCE and RDH acknowledge funding from NSF-OPP 1836839. MGC, IHM-S and BCF were funded by the EU Horizon 2020 Research and Innovations Programme through the CHARTER project (Grant #869471). MGC and IHM-S were also funded by the NERC Tundra Time project (NE/W006448/1). MGC was also funded by the EU Horizon 2020 Research and Innovations Programme under the Marie Skłodowska-Curie grant agreement No 101152158, and by the British Spanish Society Award. IHM-S was additionally funded by the Canada Excellence Research Chairs Program funded by the Natural Sciences and Engineering Research Council of Canada (NSERC). BCF was also funded by NSF Grant NNA 198230 (AROSS). 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 was supported by The Danish Council for Independent Research: Natural Sciences (DFF 4181-00565 to SN). MPB(1) was supported by the Strategic Research Environment BECC - Biodiversity and Ecosystem services in a Changing Climate. MPB(2) was supported by the National Science Foundation (ANS-2113641). 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 and the Research Council of Finland (347188). RR was supported by the Danish National Research Foundation (DNRF100 and DNRF168). PM was funded by the Estonian Academy of Sciences. AP benefited from the equipment and framework of the COMP-HUB and COMP-R Initiatives, funded by the 'Departments of Excellence' program of the Italian Ministry for University and Research (MIUR, 2018-2022 and MUR, 2023-2027). AB received funding from INTERACT (grant agreement no. 262693), under the European Community's

Seventh Framework Programme. A-MV benefited from funding from the Gordon and Betty Moore Foundation (grant #8414) and funding catalyzed by the TED Audacious Project (Permafrost Pathways). AT was funded by the Natural Resources Institute Finland. BE received financial support from the Danish National Research Foundation (CENPERM DNRF100). EL was funded by the Natural Science and Engineering Council of Canada (NSERC), ArcticNet and the Canadian International Polar Year Program, with logistical support from the Polar Continental Shelf Program. GS-S was supported by the University of Zurich Research Priority Program Global Change and Biodiversity (URPP GCB). ISJ benefited from the University of Iceland Research Fund, Icelandic Research Fund 2007. JJL was funded by the Research Foundation Flanders (FWO, grant numbers G018919N and 12P1819N) and by BiodivERsA+ (ASICS, G0H6720N). JMSD acknowledges the program RYC2022-035668-I, funded by MCIU / AEI / 10.13039 / 501100011033 and FSE+. LH was funded by Parks Canada, Weston Family Foundation. MI-G was funded by the University Research Priority Program on Global Change and Biodiversity of the University of Zurich (URPP-GCB). MCM was supported by NSF award (2224776). ML was funded by the Academy of Finland (RESICLIM; 1342890). NL was funded by NSERC, the Canada Research Chair Program, Polar Continental Shelf Project, Arcticnet, the Canadian Fund for Innovation, Polar Knowledge Canada, Government of Nunavut, and Université de Moncton. RDH was funded by the National Science Foundation (1836839). RGB was funded by the Swedish Research Council FORMAS (942-2015-1382). RHS was supported by the ERANET.RUS Treeline Project and UKLIP21 Project, Czech Republic. SEV was funded by the Australian Research Council Discovery Early Career Research Award (DE14101611). WAG was supported in part by the National Science Foundation Collaborative Research Project (1836898).

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8 Supplementary Materials

Supplementary Tables

Table Number	Table Name
Table S1	Selected functional traits
Table S2	Bayesian model structures and outputs
Table S3	Standard deviation of traits per functional group

Supplementary Methods

Method Number	Table Name
Method S1	Automated and manual trait quality control
Method S2	Trait gap-filling

Supplementary Figures

Figure Number	Figure Name
Figure S1	Plot counts by minimum number of repeats
Figure S2	Proportion of traits by gap-filling hierarchy
Figure S3	Simulations of functional richness and evenness
Figure S4	Results (**Figure 2**) including species richness
Figure S5	Functional diversity metrics vs species richness
Figure S6	Functional richness, evenness & dispersion vs precipitation
Figure S7	Functional richness, evenness & dispersion vs soil moisture
Figure S8	Functional richness, evenness & dispersion vs biogeographic region
Figure S9	Functional diversity vs functional group cover (disaggregated)
Figure S10	Results (**Figure 3**) including species richness

Figure S11	Functional richness, evenness & dispersion change vs latitude
Figure S12	Functional richness, evenness & dispersion change vs temperature
Figure S13	Functional richness, evenness & dispersion change vs precipitation
Figure S14	Functional richness, evenness & dispersion change vs precipitation change
Figure S15	Change in shrub, forb and graminoid cover

Supplementary Tables:

Table S1 | Selected functional traits. The functional traits selected for inclusion in the calculation of functional diversity metrics (**Section 2.3**; **2.5**), the ecological relevance of each trait and a selection of literature sources from which information on each trait was drawn.

Functional Trait	What it shows?	Trait Type	Literature Source(s)
Specific Leaf Area (SLA)	Ratio of leaf area to dry mass in leaves. Linked to the plant resource economic spectrum. Influences processes including resource economy, plant growth rate, evapotranspiration and plant hydrology	Continuous	Bjorkman et al. (2018a); Gross et al. (2007); Hall et al. (2020); Kazakou et al. (2016); Thomas et al. (2020; 2018); van der Plas et al. (2020); Wright et al. (2004)
Leaf Nitrogen Content (Leaf N)	Linked to the plant resource economic spectrum. Strongly linked to photosynthetic structure and capability, and resultantly CO_2 drawdown	Continuous	Bjorkman et al. (2018a); Thomas et al. (2020; 2018); Wright et al. (2004)
Leaf Phosphorus Content (Leaf P)	Linked to the plant resource economic spectrum. Impacts plant structure and growth, metabolism and physiology	Continuous	Niitynen et al. (2020); Wright et al. (2004)
Leaf Dry Matter Content (LDMC)	Measure of tissue density. Linked to the plant resource economic spectrum. Relates to nutrient stress and acquisition, and hence biomass production and growth rate.	Continuous	Bjorkman et al. (2018a); Diaz et al. (2004); Gross et al. (2007); Hall et al. (2020); Thomas et al. (2020; 2018); Wright et al. (2004)
Leaf Area	Impacts fluxes across the leaf surface, including light and carbon capture, evapotranspiration and water loss. Also impacts drought resilience	Continuous	Bjorkman et al. (2018a); Thomas et al. (2020; 2018); van der Plas et al. (2020); Wright et al. (2004)
Plant Height (vegetative)	Strongly influences competition and resistance to disturbance.	Continuous	Bjorkman et al. (2018a); Hall et al. (2020); Mayfield et al. (2010); Niitynen et al. (2020); Thomas et al. (2020; 2018)
Seed Dry Mass (SDM)	Relates significantly to plant reproductive output and hence, resistance, colonisation and community composition	Continuous	Kidson and Westoby (2000); Parker et al. (2006); Niitynen et al. (2020); Thomas et al. (2020; 2018); Walters and Reich (2000)
Woodiness	Influences plant structure, decomposition patterns, and resistance to environmental extremes and disturbance	Categorical	Bjorkman et al. (2018a); Cornwell et al. (2008; 2009); FitzJohn et al. (2014); Hall et al. (2020); Zanne et al. (2014)
Lifespan / Evergreenness	Influences decomposition patterns, and resistance to environmental extremes and disturbance	Categorical	Bjorkman et al. (2018a); Cornwell et al. (2008; 2009); FitzJohn et al. (2014); Hall et al. (2020); Zanne et al. (2014)

Table S2 | Bayesian model structures. The structure and output of each individual Bayesian model run as part of the analyses for this study. Where applicable (categorical models only), the grouping level is listed next to the relevant outputs. ‘CI’ refers to the model’s credible intervals. Models listed with a star (*) in the right hand column highlight when the 95% CIs for the main predictor variable do not overlap zero (excluding categorical variables) and hence can be considered to have a ‘significant’ effect.

Model	Model structure	Group	Estimate	Error	Lower 95% CI	Upper 95% CI	
1	FRic ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0331	0.0162	-0.0656	-0.0017	*
2	FEve ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0042	0.0023	-0.0004	0.0088	
3	FDis ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0027	0.0085	-0.0192	0.0143	
4	SR ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0278	0.0115	-0.0501	-0.0052	*
5	FRic ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0675	0.0267	0.0144	0.1192	*
6	FEve ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0142	0.0034	-0.0205	-0.0074	*
7	FDis ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0050	0.0147	-0.0239	0.0338	
8	SR ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0641	0.0184	0.0278	0.0993	*
9	FRic ~ ForbCover + I(ForbCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00023	0.00002	-0.00028	-0.00019	*
10	FRic ~ GraminoidCover + I(GraminoidCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00021	0.00002	-0.00024	-0.00018	*
11	FRic ~ ShrubCover + I(ShrubCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00017	0.00002	-0.00021	-0.00014	*
12	FEve ~ ForbCover + I(ForbCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00002	0.00001	-0.00004	0.00000	
13	FEve ~ GraminoidCover + I(GraminoidCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00004	0.00001	-0.00005	-0.00003	*
14	FEve ~ ShrubCover + I(ShrubCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00004	0.00001	-0.00005	-0.00003	*
15	FDis ~ ForbCover + I(ForbCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00030	0.00002	-0.00035	-0.00026	*
16	FDis ~ GraminoidCover + I(GraminoidCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00032	0.00001	-0.00034	-0.00029	*
17	FDis ~ ShrubCover + I(ShrubCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00034	0.00001	-0.00037	-0.00031	*
18	SR ~ ForbCover + I(ForbCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00021	0.00002	-0.00025	-0.00017	*
19	SR ~ GraminoidCover + I(GraminoidCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00015	0.00001	-0.00018	-0.00012	*
20	SR ~ ShrubCover + I(ShrubCover^2) + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.00014	0.00001	-0.00016	-0.00011	*
21	FRic ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0003	0.0002	-0.0001	0.0007	
22	FEve ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0000	0.0000	-0.0001	0.0000	

23	FDis ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0000	0.0001	-0.0003	0.0002	
24	SR ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0003	0.0002	0.0000	0.0006	*
25	FRic ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Dry (Base)	2.66	0.11	2.45	2.88	
	FRic ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Moist	0.15	0.10	-0.05	0.36	
	FRic ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Wet	-0.30	13.00	-0.30	0.23	
26	FEve ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Dry (Base)	0.57	0.02	0.53	0.61	
	FEve ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Moist	0.00	0.02	-0.04	0.05	
	FEve ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Wet	-0.03	0.03	-0.09	0.03	
27	FDis ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Dry (Base)	2.13	0.09	1.96	2.30	
	FDis ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Moist	0.08	0.09	-0.10	0.26	
	FDis ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Wet	-0.28	0.13	-0.54	-0.03	
28	SR ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Dry (Base)	1.97	0.10	1.77	2.16	
	SR ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Moist	0.14	0.09	-0.03	0.32	
	SR ~ Moisture + log(PlotSize) + (1|Gridcell/Subsite)	Wet	-0.08	0.12	-0.31	0.16	
29	FRic ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	Eurasia (Base)	2.57	0.18	2.21	2.92	
	FRic ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	GreenIceland	0.24	0.22	-0.20	0.68	
	FRic ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-E	0.03	0.27	-0.50	0.55	
	FRic ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-W	0.13	0.28	-0.41	0.68	
30	FEve ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	Eurasia (Base)	0.52	0.02	0.48	0.57	
	FEve ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	GreenIceland	0.04	0.03	-0.01	0.09	
	FEve ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-E	0.10	0.04	0.03	0.16	
	FEve ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-W	0.10	0.03	0.04	0.17	
31	FDis ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	Eurasia (Base)	2.01	0.08	1.86	2.17	
	FDis ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	GreenIceland	-0.04	0.10	-0.24	0.15	

	FDis ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-E	0.19	0.13	-0.08	0.45
	FDis ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-W	0.27	0.13	0.01	0.51
32	SR ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	Eurasia (Base)	1.97	0.13	1.71	2.24
	SR ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	GreenIceland	0.10	0.16	-0.21	0.42
	SR ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-E	-0.14	0.19	-0.51	0.24
	SR ~ Region + log(PlotSize) + (1|Gridcell/Subsite)	N. America-W	0.03	0.20	-0.37	0.42
33	FRic Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0128	0.0446	-0.1024	0.0749
34	FEve Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0009	0.0011	-0.0030	0.0013
35	FDis Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0013	0.0039	-0.0062	0.0095
36	SR Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0081	0.0159	-0.0389	0.0236
37	FRic Change ~ Temp. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-4.5869	3.2423	-10.8452	1.8692
38	FEve Change ~ Temp. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0236	0.0762	-0.1251	0.1710
39	FDis Change ~ Temp. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-1.4050	1.1184	-3.6796	0.7015
40	SR Change ~ Temp. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-1.3791	1.1505	-3.7276	0.8198
41	FRic Change ~ Precip. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0062	0.0108	-0.0149	0.0278
42	FEve Change ~ Precip. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0004	0.0003	-0.0009	0.0001
43	FDis Change ~ Precip. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0029	0.0038	-0.0047	0.0102
44	SR Change ~ Precip. Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0030	0.0039	-0.0047	0.0104
45	FRic Change ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0074	0.0083	-0.0244	0.0089
46	FEve Change ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0004	0.0002	-0.00003	0.0008
47	FDis Change ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0038	0.0030	-0.0101	0.0019
48	SR Change ~ Latitude + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0037	0.0029	-0.0098	0.0019
49	FRic Change ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0095	0.0139	-0.0176	0.0363
50	FEve Change ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0005	0.0003	-0.0012	0.0001

51	FDis Change ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0060	0.0046	-0.0028	0.0151	
52	SR Change ~ Temperature + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0061	0.0044	-0.0026	0.0148	
53	FRic Change ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0000	0.0001	-0.0003	0.0003	
54	FEve Change ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0000	0.0000	-0.00001	0.00000	
55	FDis Change ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0000	0.0001	-0.0001	0.0001	
56	SR Change ~ Precipitation + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0000	0.0001	-0.0001	0.0001	
57	ShrubCover Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0929	0.1648	-0.2528	0.3953	
58	ForbCover Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0225	0.1034	-0.1781	0.2259	
59	GraminoidCover Change ~ 1 + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.1129	0.1482	-0.3898	0.1854	
60	FRic Change ~ ForbCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.1083	0.0155	0.0782	0.1387	*
61	FRic Change ~ ShrubCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0527	0.0120	-0.0762	-0.0295	*
62	FRic Change ~ GraminoidCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0068	0.0122	-0.0302	0.0174	
63	FEve Change ~ ForbCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0028	0.00064	0.0017	0.0039	*
64	FEve Change ~ ShrubCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0005	0.0004	-0.0013	0.0002	
65	FEve Change ~ GraminoidCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0009	0.0004	-0.0017	-0.0001	*
66	FDis Change ~ ForbCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0418	0.0051	0.0318	0.0518	*
67	FDis Change ~ ShrubCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.01714	0.0039	-0.0247	-0.0096	*
68	FDis Change ~ GraminoidCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0056	0.0041	-0.0137	0.0022	
69	SR Change ~ ForbCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	0.0419	0.0051	0.0316	0.0515	*
70	SR Change ~ ShrubCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0170	0.0039	-0.0245	-0.0092	*
71	SR Change ~ GraminoidCover Change + log(PlotSize) + (1|Gridcell/Subsite)	-	-0.0057	0.0039	-0.0133	0.0018	

Table S3 | Standard deviation of trait values per functional group. Highlighted values represent the most variable functional group for each of the seven continuous traits used in this analysis.

	LDMC	**LeafN**	**LeafP**	**Leaf_Area**	**Height**	**SDM**	**SLA**
Forb	0.08	13.52	1.20	2597.23	0.11	3.28	9.63
Graminoid	0.11	11.70	0.97	343.10	0.11	0.35	6.37
Shrub	0.10	10.79	1.05	771.56	2.44	5.52	14.12

Supplementary Methods:

Method S1 | Description of automated and manual quality control carried out on the combined trait dataset. A concise description of the trait data used, where it was sourced and how we selected the traits in question can be found in **Section 2.3**.

Duplicate records, both within and between the TTT and TRY datasets were checked for and removed. Histograms were also generated for all species-trait combinations to identify significant outliers and clusters of erroneous data points requiring removal. All trait values that fell outside two standard deviations of the mean trait value for that species-trait combination were removed automatically, whilst rare clusters of clearly incorrect values were filtered from the dataset. Leaf area values displayed numerous clusters of incorrect values due to the apparent inclusion of ‘leaflet areas’ as ‘single leaf areas’. To rectify this issue, k-means clustering (n = 2) was run on all species-leaf area combinations. If the distance between the means of the two respective clusters was greater than 50% of the spread of all the data for that species-leaf area combination, the cluster of larger areas was deemed likely to be a ‘leaflet area’ and was thus precautionarily removed. The combined dataset also contained both vegetative and reproductive plant height records so additional checks were run to ensure the most suitable height records were being retained. For each species, if the number of vegetative records was four or greater, only vegetative records were retained. If it was less than four, but there was four or more reproductive records, reproductive records were considered a more accurate representation and retained. If there were less than four records for both height types, all height records were removed for that species due to low confidence in the remaining values.

Method S2 | Description of the gap-filling process carried out on the combined trait dataset. A concise description of the gap-filling process used on the trait data can be found in **Section 2.4**.

To estimate missing trait values, we used a hierarchical gap filling algorithm that works across two different hierarchical scales, with trait medians being generated across a spatial (S) hierarchy within each taxonomic (T) hierarchical unit (Figure S2a) so as to keep as much as possible the raw information on intraspecific trait variation. For each trait per species record per plot, trait medians are generated first at the species level (T1), followed by the genus (T2), family (T3) and functional group levels (T4; shrub, forb and graminoid; Figure S2a). Within each of these taxonomic levels, trait medians are generated across a progressively widening spatial hierarchy (Figure S2a). For each record, calculations occur first within the relevant 0.5 ° × 0.5 ° latitude-longitude grid cell (S1), followed by the 5 ° latitudinal band of the source within the biogeographic region (S2), over 60 °N within the biogeographic region of the source (S3), the wider biogeographic region (S4), the wider continent of the source (S5; e.g., Eastern and Western North America become simply North America, Greenland-Iceland remains as Greenland-Iceland) and finally, global (S6; Figure S2a). The progression of hierarchical units from most to least specific hence runs: T1:S1 (species: gridcell), T1:S2, [...], T2:S1, T2:S2, […] up to T4:S6 (functional group:global; Figure S2b).

For the second step, median trait values were always selected at the finest hierarchical level possible (Figure S2b). In order to ensure the accuracy and representativeness of the median trait value, a threshold based on the number of trait records within the given hierarchical unit (numR) and Z-score had to be met for a median to be selected. If that threshold was not met, the algorithm moves on to the next hierarchical unit and so on until the thresholds are met and a median trait value is selected. If for a given trait record $Z < 2.25$ and $4 \le numR < 10$, it was retained. Moving upwards, individual trait records were also retained when $2.25 \le Z < 2.75$ and $10 \le numR < 20$, when $2.75 \le Z < 3.25$ and $20 \le numR < 30$ and when $Z < 4$ and $numR \ge 30$. Any record with $Z \ge 4$ was removed. From the remaining dataset, for each composition record and trait, the median trait value from the narrowest hierarchical unit with at least four records remaining was used. This results in a dataset with a single value for each of the seven continuous traits ascribed to each composition record. On average, 64.1% of trait values were drawn from species-level trait values (T1:S1-6), with height (84.1%) and SDM (39.9%) incorporating the highest and lowest proportion of species data respectively (Figure S2c). Categorical values for ‘evergreenness’ and ‘woodiness’ (e.g. 0 or 1) were then added for each composition record but as these traits were calculated from functional group classifications (evergreen shrubs = evergreen, others not; all shrubs = woody, other not), gap-filling was not required (Bjorkman et al., 2018a). The full workflow along with details of the proportion of trait values gap-filled at each spatial and taxonomic level can be seen in Figure S2.

Supplementary Figures:

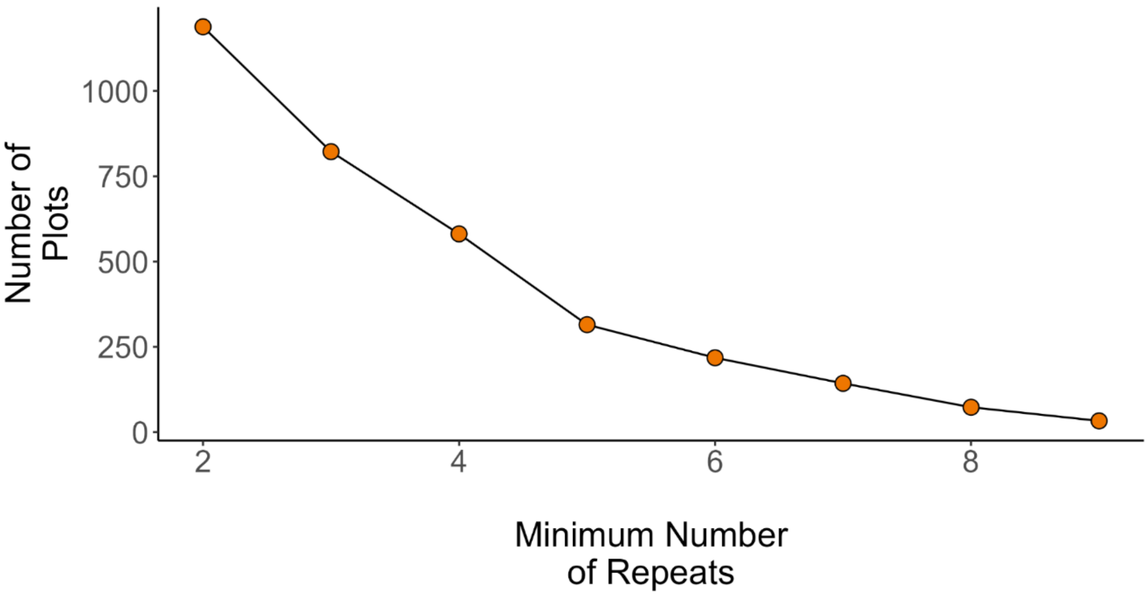


Figure S1 | Dataset size vs number of repeats. Total plot count in the temporal dataset depending on the minimum number of repeats stipulated for inclusion.

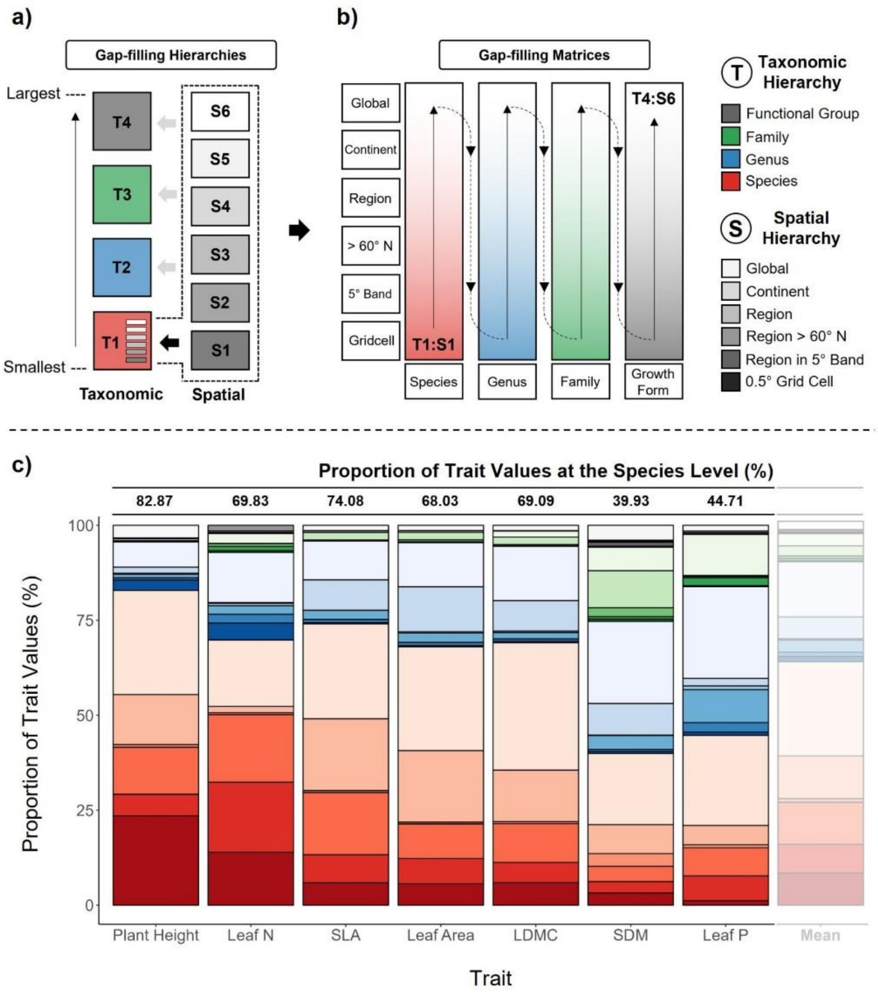
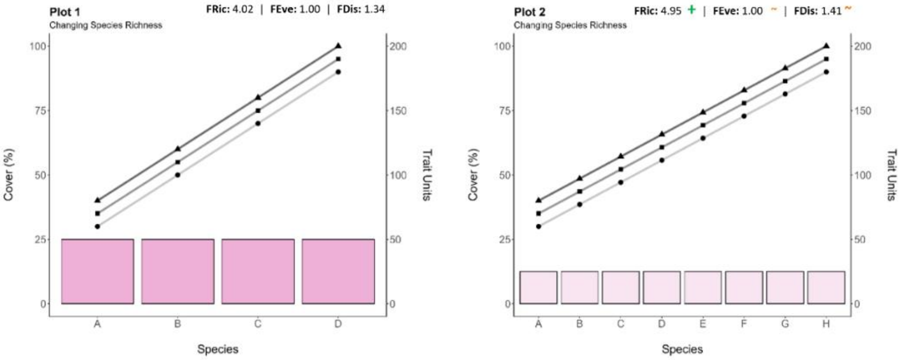
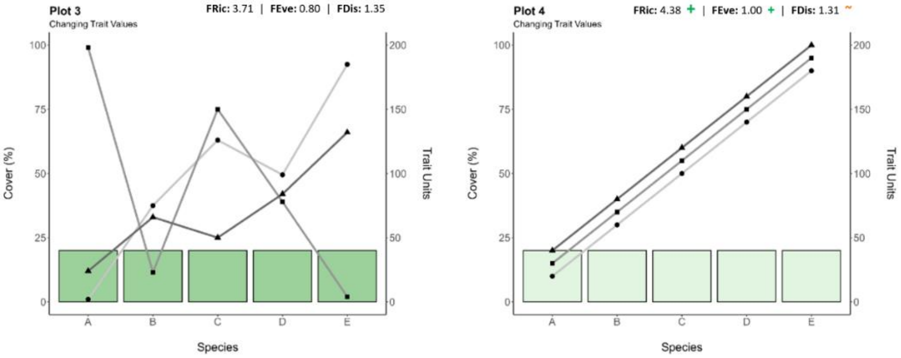


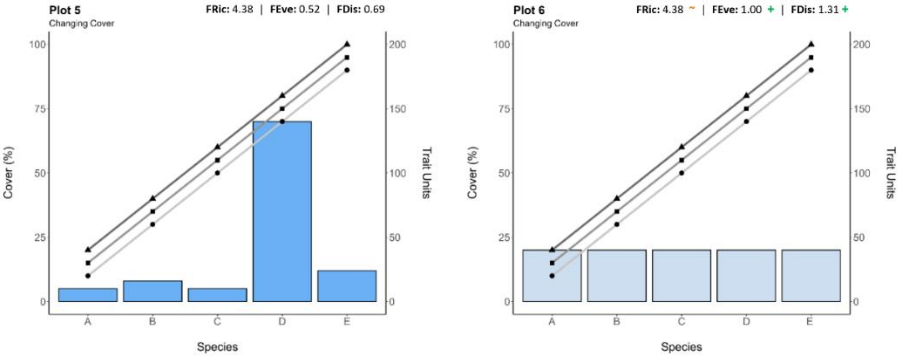
Figure S2 | Proportion of trait medians per continuous trait drawn from each hierarchical gap-filling level. a) The nesting of the spatial hierarchical levels (6) within each of the taxonomic hierarchical units (4). **b)** The order in which values were gap-filled, progressing through each spatial unit within a single taxonomic unit before then moving onto the next taxonomic unit. **c)** As per the methods above, each composition record was assigned a median trait value for each of the seven continuous traits at the lowest taxonomic and spatial hierarchical unit possible whilst satisfying criteria concerning the number of records and Z-score associated with its calculation. Woodiness and evergreenness were not included in this plot as they were derived from functional group classifications. This plot highlights the proportion of records per trait that were sampled from each spatial hierarchical unit within each taxonomic hierarchical unit. The overall proportion of trait medians sampled from across all six species units per trait (red bars) are highlighted at the top, ranging from a maximum of 82.87% for plant height to just 39.93% for SDM, with a mean proportion of 64.08% (right-hand bar). Trait abbreviations in the x-axis labels are: Leaf N (leaf nitrogen), SLA (specific leaf area), LDMC (leaf dry-matter content), SDM (seed dry mass) and Leaf P (leaf phosphorus).



	Plot 1	Plot 2	Change (%)	Illustrates...
FRic	4.02	4.95	**23.13**	*FRic influenced significantly by increased species richness*
FEve	1	1	**0**	*FEve not influenced by changes in species richness, fully independent of species richness*
FDis	1.34	1.41	**5.22**	*FDis only minimally influenced by species richness, far more independent than FRic*



	Plot 3	Plot 4	Change (%)	Illustrates...
FRic	3.71	4.38	**18.06**	*FRic influenced by changing distribution of trait values within trait space*
FEve	0.8	1	**25**	*FEve influenced by changing distribution of trait values within trait space*
FDis	1.35	1.31	**-2.96**	*FDis only minimally influenced, likely due to similar overall dispersion from centroid values*



	Plot 5	Plot 6	Change (%)	Illustrates...
FRic	4.38	4.38	**0**	*FRic not influenced, fully independent from changes in abundance*
FEve	0.52	1	**92.31**	*FEve very strongly affected by changes in the relative abundance of species within a plot*
FDis	0.69	1.31	**89.86**	*FDis very strongly affected by changes in the relative abundance of species within a plot*

Figure S3 | Simulations of functional richness, evenness and dispersion. Figures produced from simulated datasets highlighting how all three calculated functional diversity metrics change when altering plot-level species richness, trait inputs and relative cover. For more discussion of this, see **Section 2.5**.

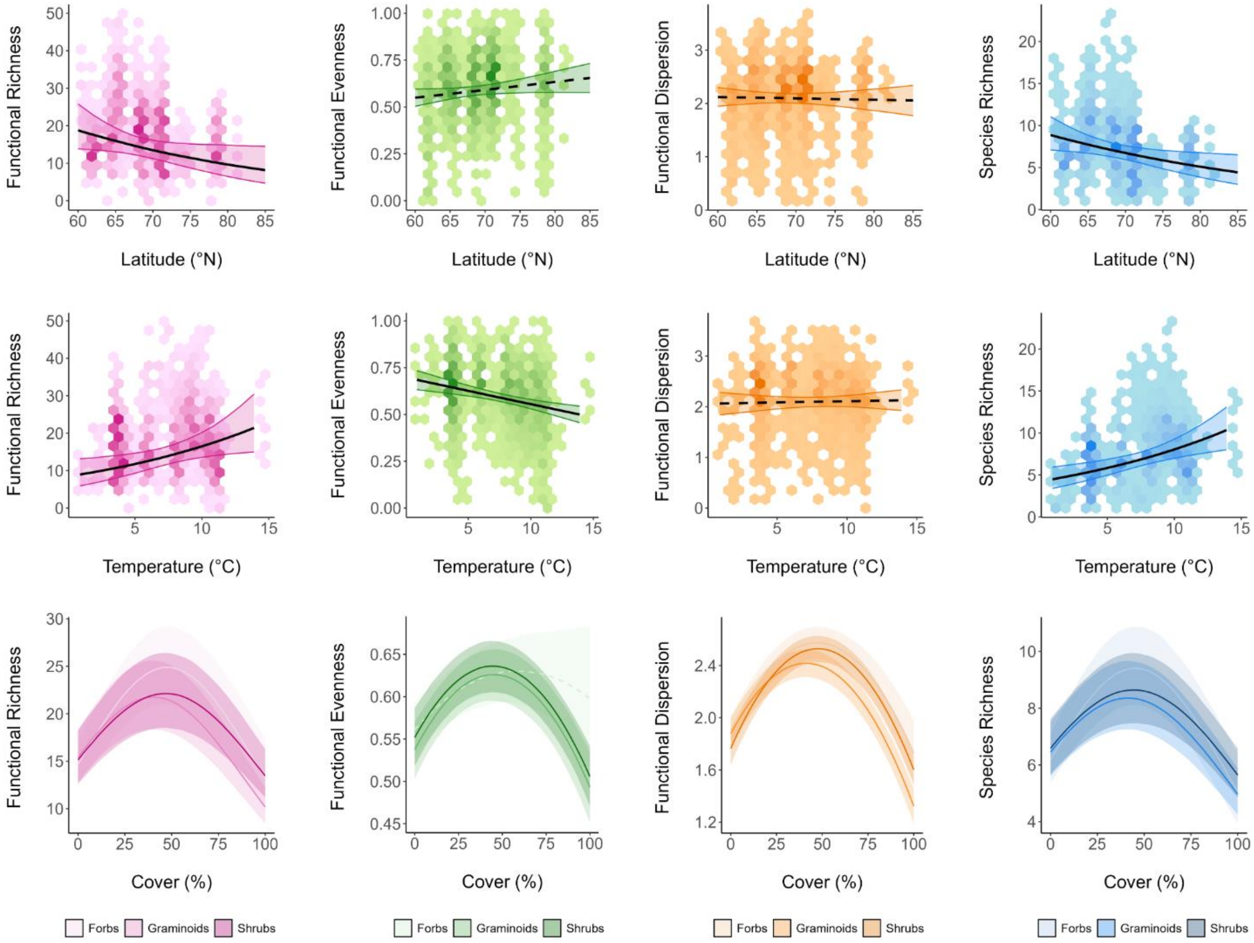


Figure S4 | Results of Figure 2 *including* species diversity. This figure highlights much the same information as **Figure 2**, whilst also incorporating results for species richness from similarly constructed models. Results for species richness generally parallel that found in García Criado et al. (2025b), *Nature*, which used a largely overlapping dataset.

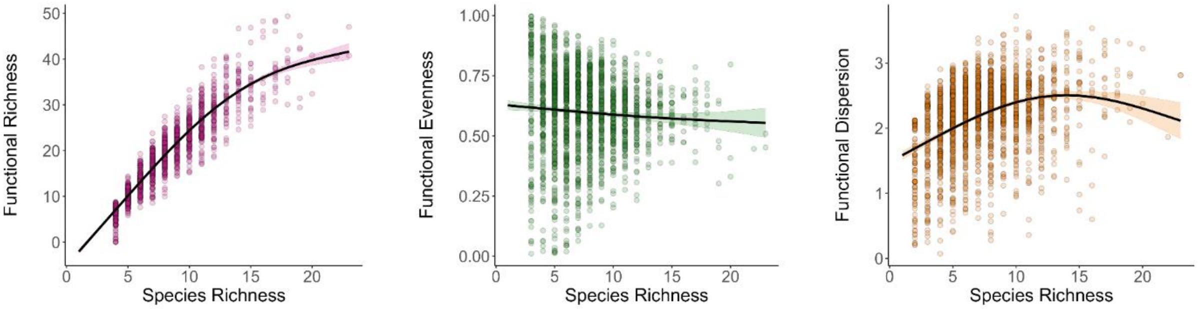
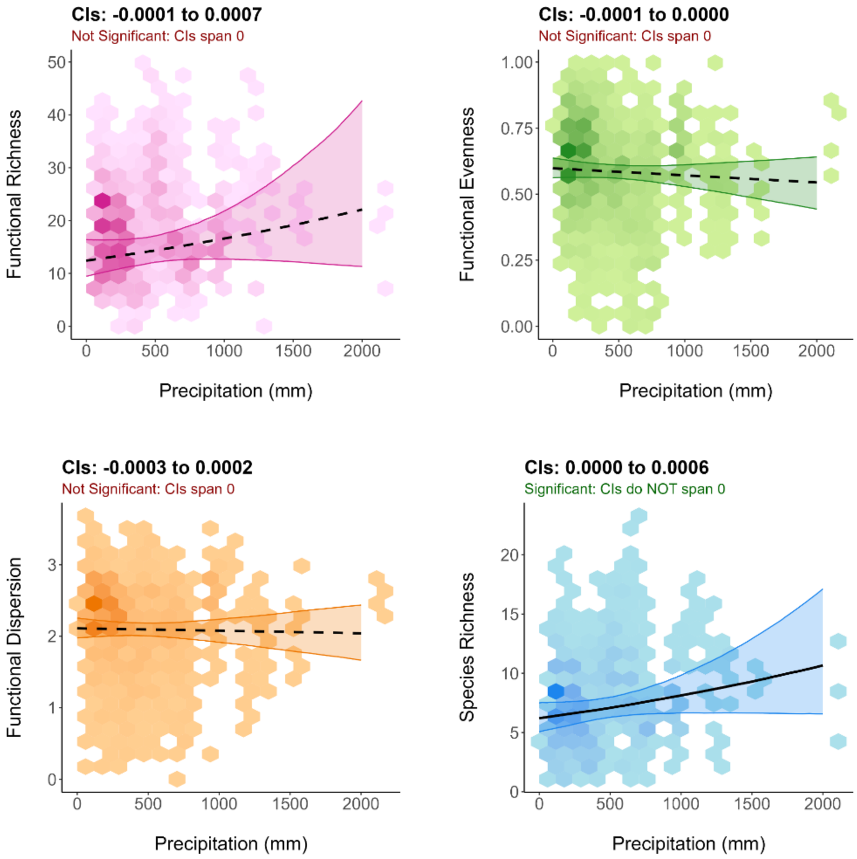


Figure S5 | Functional diversity vs species richness. The outputs of Generalised Additive Models (GAMs) highlighted the strong, known relationship between functional richness and species richness, the weaker relationship between functional dispersion and species richness, and apparent lack of relationship between functional evenness and species richness.


CIs: -0.0001 to 0.0007
Not Significant: CIs span 0

CIs: -0.0001 to 0.0000
Not Significant: CIs span 0

CIs: -0.0003 to 0.0002
Not Significant: CIs span 0

CIs: 0.0000 to 0.0006
Significant: CIs do NOT span 0

Figure S6 | Functional diversity vs precipitation. Model outputs (including 95% CIs) of the relationships between functional richness, evenness and dispersion, and species richness with annual precipitation. Details of the annual precipitation variable can be found in **Section 2.2**, mention of this result can be found in **Section 3.1**, whilst details of the specific models run can be found in **Section 2.6.1** and **Table S2**.

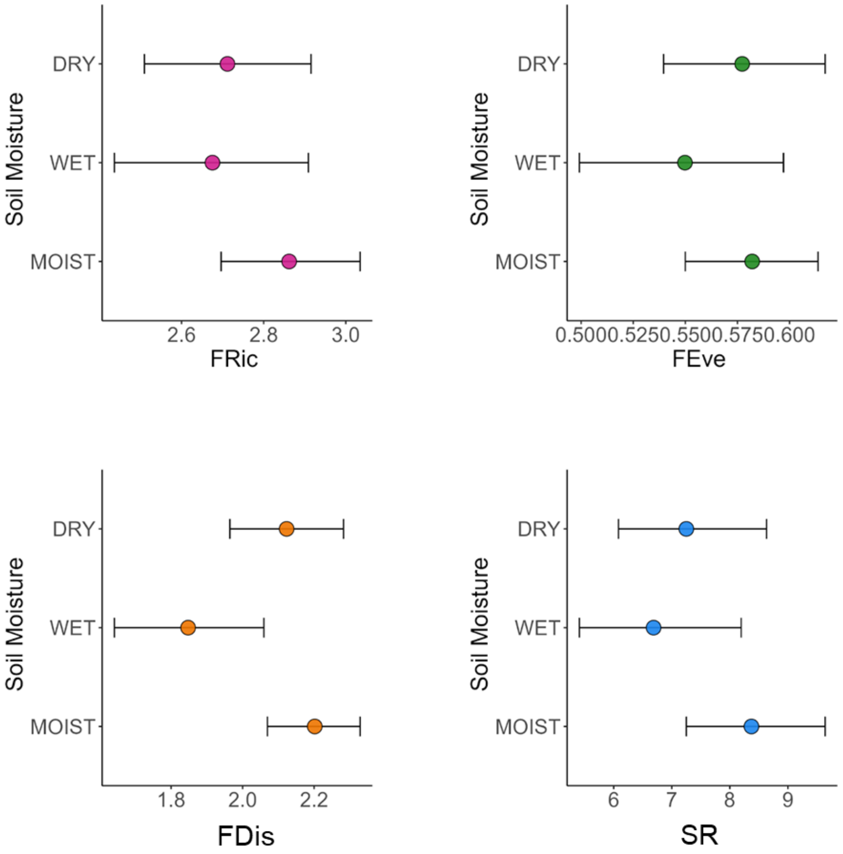


Figure S7 | Functional diversity vs soil moisture. Model outputs (including 95% CIs) of the relationships between functional richness, evenness and dispersion, and species richness with categorical soil moisture. Details of the soil moisture variable can be found in **Section 2.2**, mention of this result can be found in **Section 3.1**, whilst details of the specific models run can be found in **Section 2.6.1** and **Table S2**.

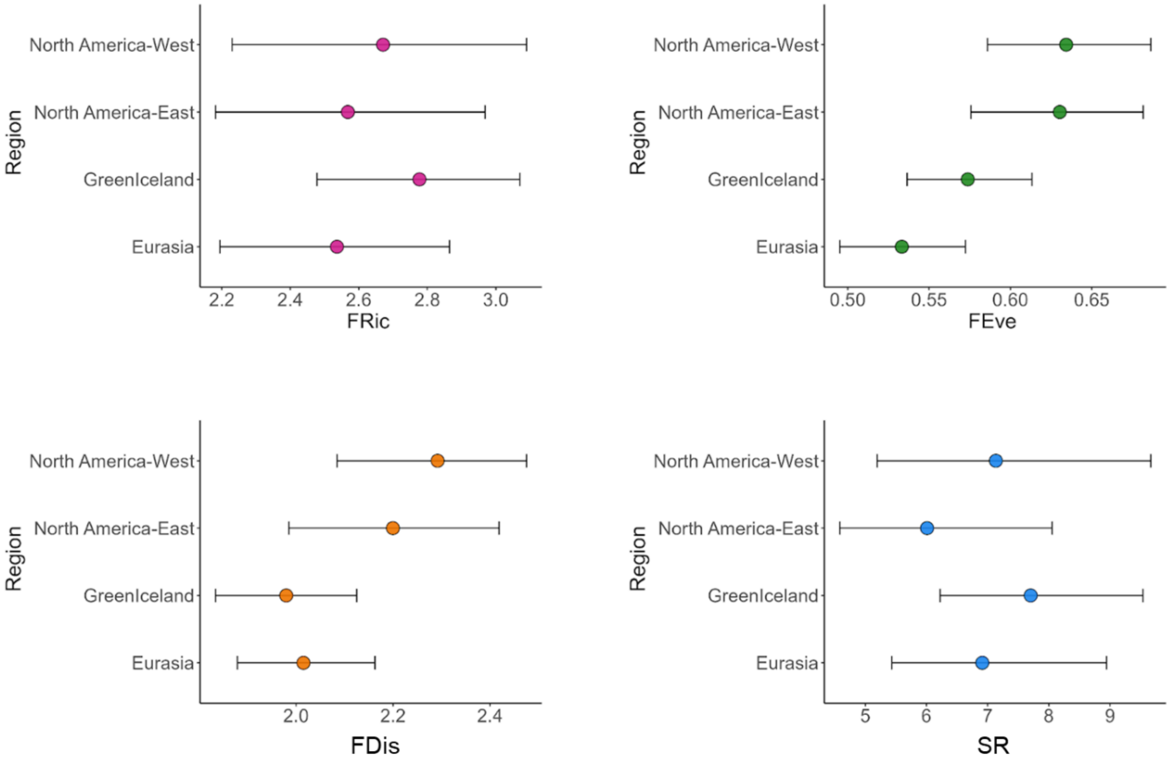


Figure S8 | Functional diversity vs biogeographic region. Model outputs (including 95% CIs) of the relationships between functional richness, evenness and dispersion, and species richness with categorical biogeographical regions. Details of the region variable can be found in **Section 2.1** and **Figure 1**, mention of this result can be found in **Section 3.1**, whilst details of the specific models run can be found in **Section 2.6.1** and **Table S2**.

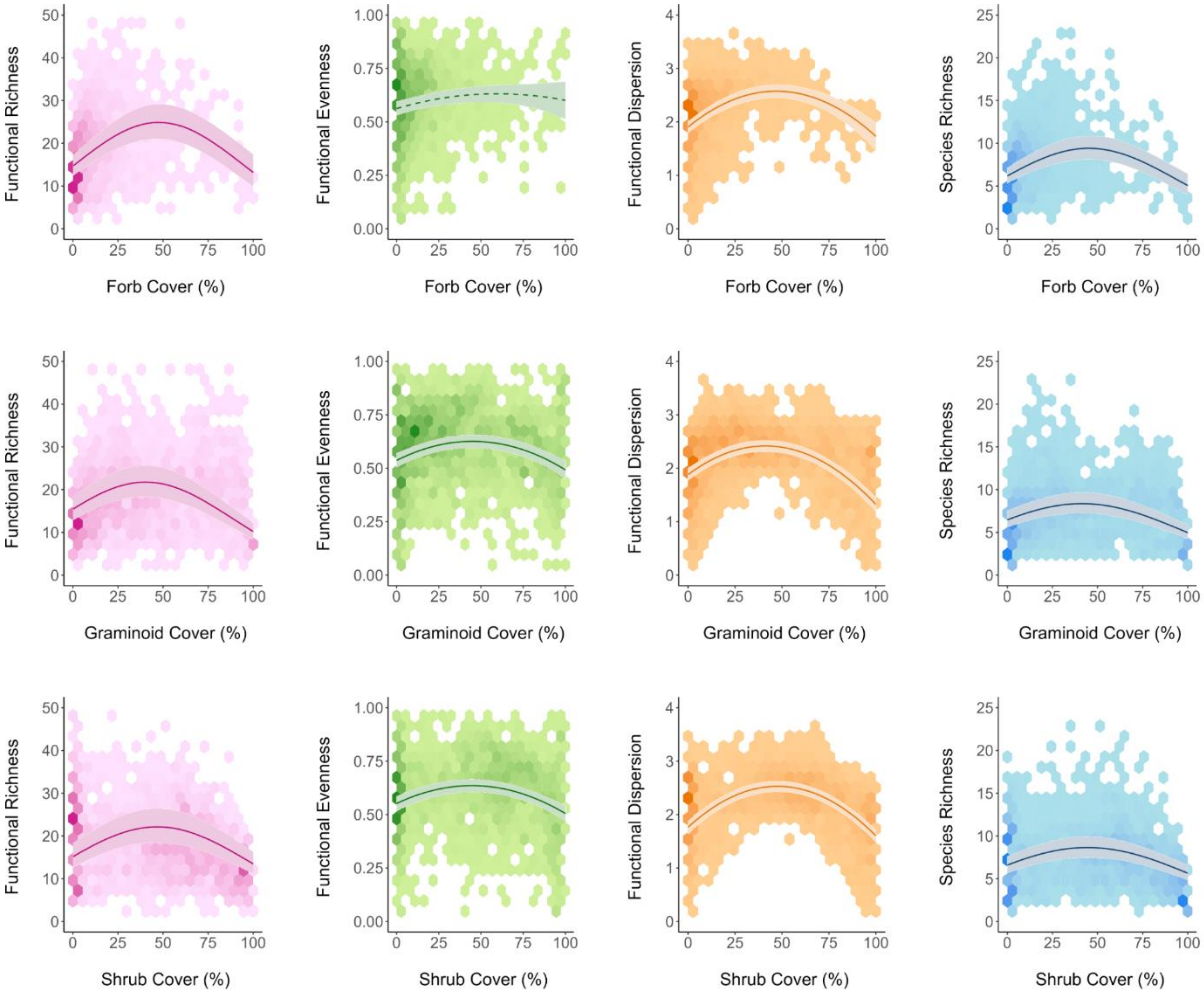


Figure S9 | Functional diversity vs functional group cover (disaggregated). Model outputs (including 95% CIs) of the relationships between functional richness, evenness and dispersion, and species richness with forb, graminoid and shrub cover. The plots are the same as those that, when combined, comprise **Figures 2g, h** and **i**. Lines and ribbons are drawn from the model outputs in **Table S2**. CIs represent the 95% CIs on the quadratic term of the model outputs in **Table S2** (solid line = 95% CIs do not overlap zero; dashed line = 95% CIs overlap zero). Hexbin colours represent the number of plots within each bin.

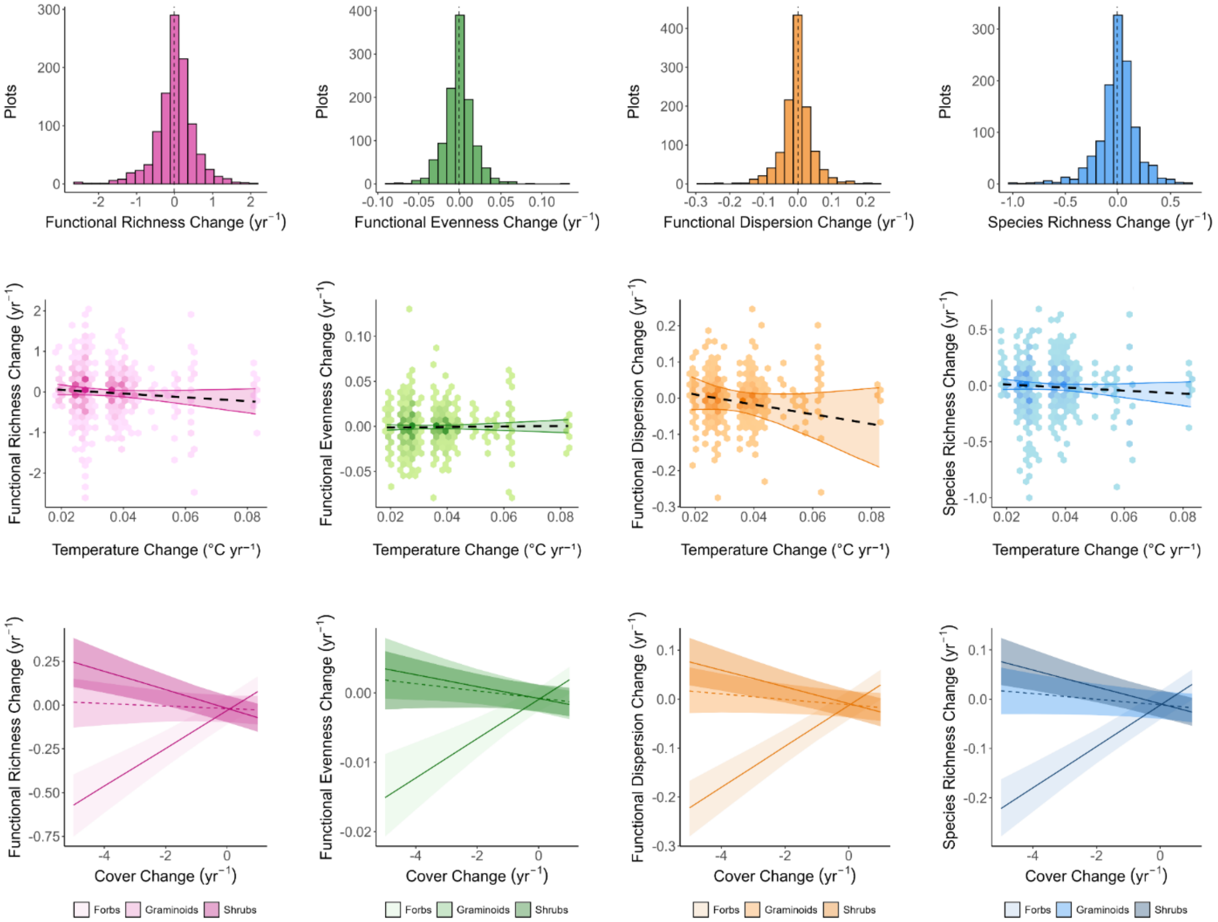


Figure S10 | Results of Figure 3 *including* species diversity. This figure highlights much the same information as **Figure 3**, whilst also incorporating results for species richness from similarly constructed models. Results for species richness generally parallel that found in García Criado et al. (2025b), *Nature*, which used a largely overlapping dataset.

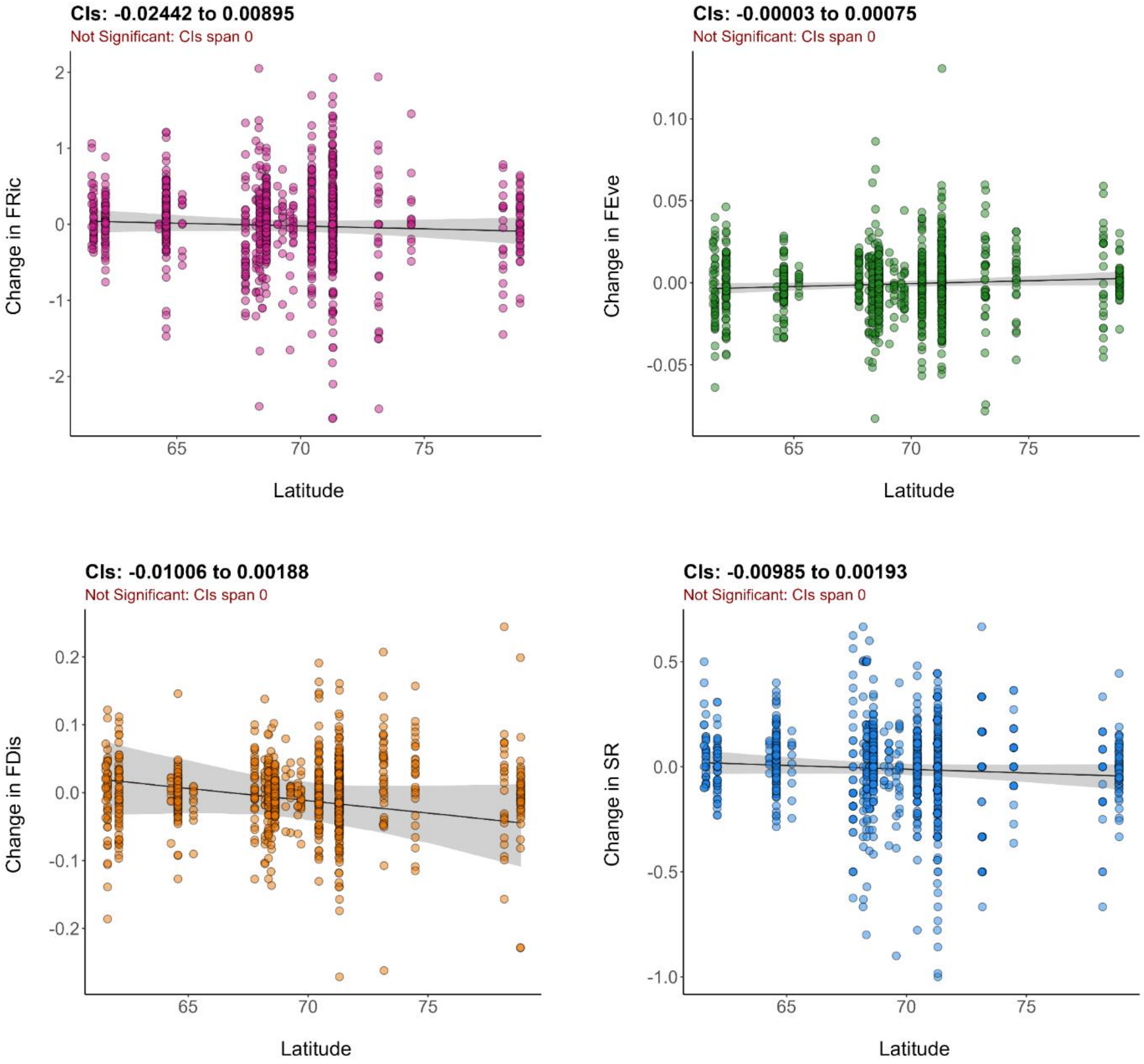


Figure S11 | Functional diversity change vs latitude. Model outputs (including 95% CIs) of the relationships between change in functional richness, evenness and dispersion, and species richness with latitude**.** Mention of this result can be found in **Section 3.2**, whilst details of the specific models run can be found in **Section 2.6.2** and **Table S2**.

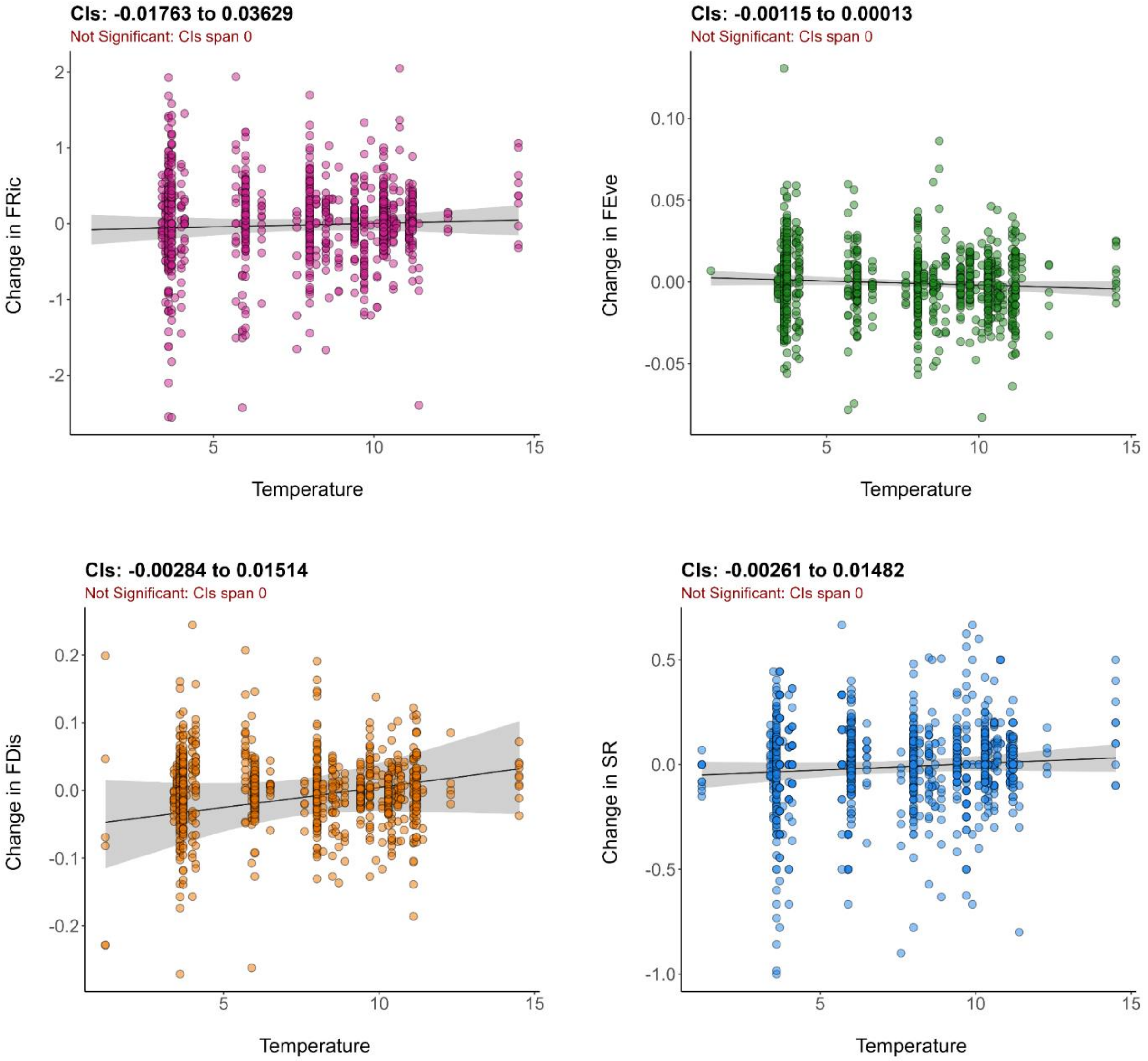


Figure S12 | Functional diversity change vs temperature. Model outputs (including 95% CIs) of the relationships between change in functional richness, evenness and dispersion, and species richness with temperature. Details of the temperature variable can be found in **Section 2.2**, mention of this result can be found in **Section 3.2**, whilst details of the specific models run can be found in **Section 2.6.2** and **Table S2**.

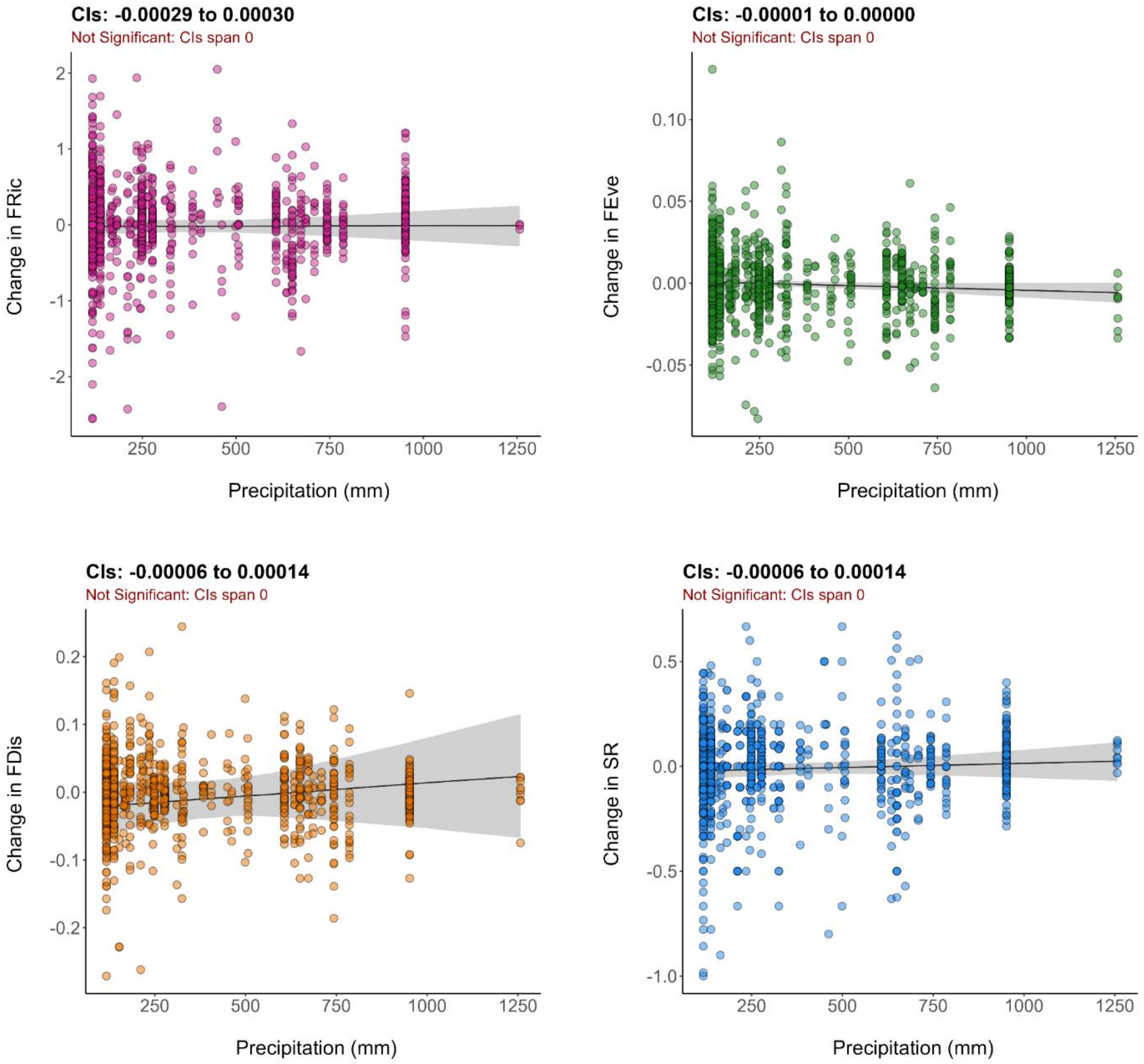


Figure S13 | Functional diversity change vs precipitation. Model outputs (including 95% CIs) of the relationships between change in functional richness, evenness and dispersion, and species richness with annual precipitation. Details of the precipitation variable can be found in **Section 2.2**, mention of this result can be found in **Section 3.2**, whilst details of the specific models run can be found in **Section 2.6.2** and **Table S2**.

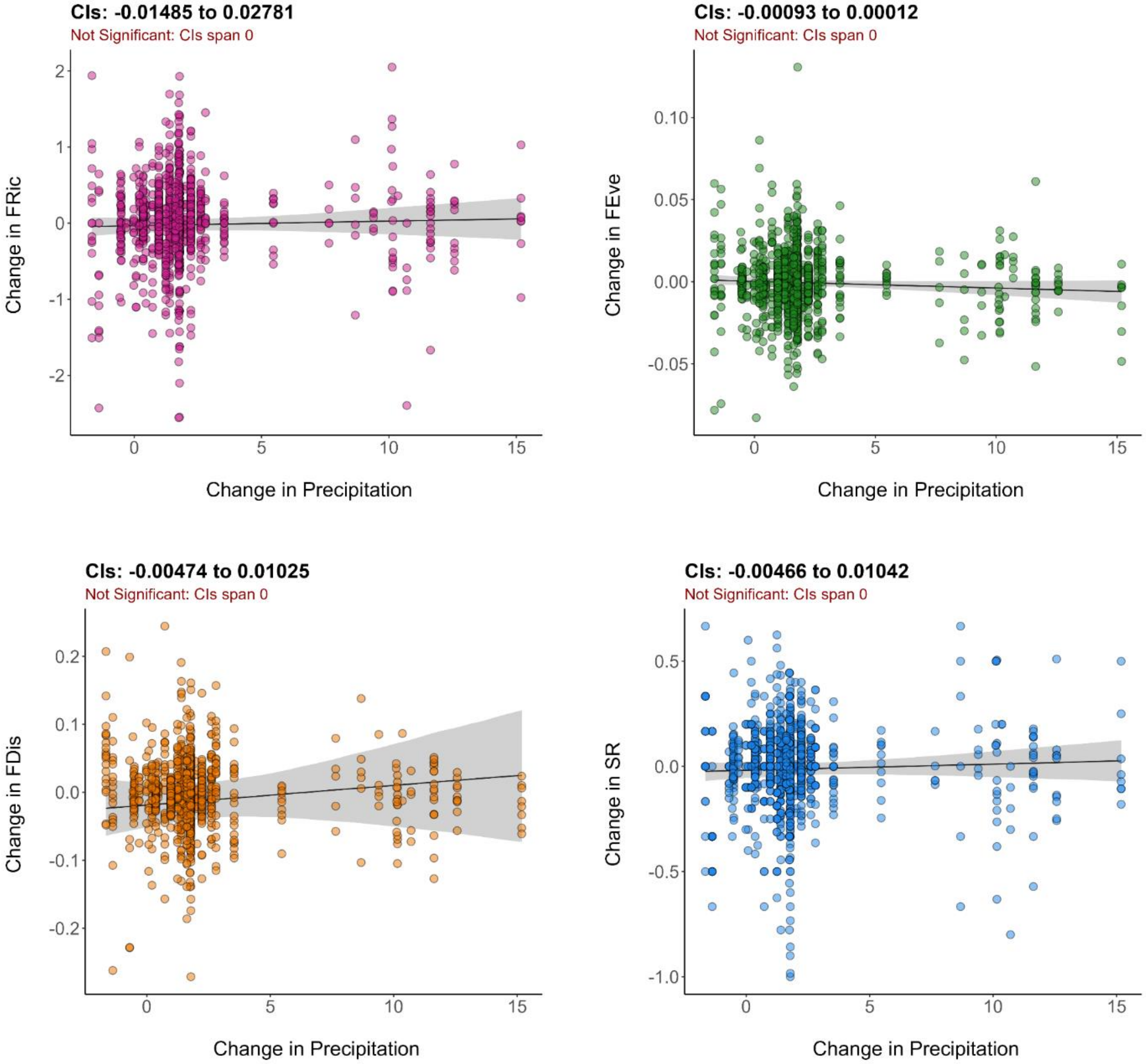


Figure S14 | Functional diversity change vs precipitation change. Model outputs (including 95% CIs) of the relationships between change in functional richness, evenness and dispersion, and species richness with change in precipitation. Details of the precipitation variable can be found in **Section 2.2**, with descriptions of how it was calculated to be found in **Section 2.6.2**, mention of this result can be found in **Section 3.2**, whilst details of the specific models run can be found in **Section 2.6.2** and **Table S2**.

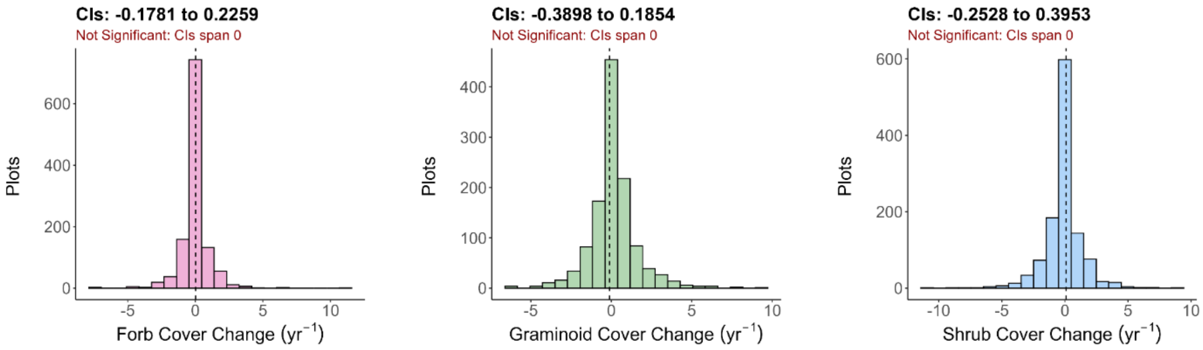


Figure S15 | Change in shrub, forb and graminoid cover over time. Model outputs (including 95% CIs) highlighting the lack of net change in shrub, forb and graminoid cover over time. Details of how this change was calculated can be found in **Section 2.6.2**.