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Research

Climate and land-use drive the functional composition of vascular plant assemblages across Norway

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Traditionally, biogeography has described the distribution of species. But as plant functional traits and functional diversity underpin ecosystem dynamics, understanding drivers of functional diversity at biogeographical scales is essential to understand spatial variation in ecosystem characteristics, particularly in light of ongoing environmental changes. Here we investigate geographic patterns of functional diversity and -traits of the Norwegian flora. We explore whether climate, land-use or glacial history are important drivers of functional diversity. We combine species occurrence records and assemblage-means of functional traits to assess the spatial distribution of functional traits and -diversity of native vascular plants in Norway in a 20 × 20 km grid. We use multiple-model inference to identify which environmental factors contribute the most in explaining the spatial patterns of trait distributions and functional diversity. Additionally, we use the constructed models to predict potential changes in distributions of traits and functional diversity given different climate change scenarios.

Both individual traits and functional diversity display clear geographic patterns, predictable by climate, landscape and glacial history. Traits related to plant size and growth peak in warmer areas and are predicted to increase in the future, as is functional richness and dispersion. In contrast, functional evenness peaks in northern regions and is predicted to decrease in the future.

The different environmental drivers vary in degree of importance, effect sizes and -directions on the assemblage-averaged functional traits and -diversity. This underlines the importance of multiple drivers in determining plant assemblage functionality. In the face of climate- and land-use change, Norway is expected to become warmer, wetter and experience a substantial increase in anthropogenic land-uses, such as increased urbanisation. In turn, the functional composition of the Norwegian flora is predicted to shift towards tall, woody, fast-growing species.

Keywords: assemblage composition, biogeography, climate change, functional diversity, functional traits, land-use



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Introduction

Biogeography has traditionally described distributions of species. For ecosystem dynamics, however, the functions species perform are of high importance as well (Violle et al. 2014). Describing and explaining distributions of species' traits is crucial for understanding how ecosystem characteristics vary in space—functional biogeography is the study of the geographic distribution of trait diversity across organisational levels (sensu Violle et al. 2014). Plants play a central role in driving ecosystem functions, and there is an increasing interest in mapping functional traits of plant assemblages (Reichstein et al. 2014, Newbold et al. 2015, Violle et al. 2015, Funk et al. 2017, Bruelheide et al. 2018, Echeverría-Londoño et al. 2018).

The ranges and distributions of functional traits in plant assemblages illustrate the abundance and diversity of strategies employed by co-occurring species (Violle et al. 2015). Traits such as height, leaf size, chemical characteristics and reproduction strategies drive numerous ecosystem functions from albedo, hydrology and microclimate (Myers-Smith et al. 2011, 2019b) to productivity, decomposition and carbon storage (Díaz et al. 2004, Cornelissen et al. 2007, Cornwell et al. 2008), as well as species interactions (Carmona et al. 2011, Rosas-Guerrero et al. 2014, Gusmão et al. 2020). Generally, functional traits are divided into 'response traits, which predict how species will react to environmental change, and 'effect traits', which affect ecosystem processes and functioning (Lavorel and Garnier 2002, Funk et al. 2017). The community remaining after any type of environmental change will be determined by the suite of response traits displayed by the original assemblage. Subsequent changes in ecosystem functioning, on the other hand, will be determined by how the changed assemblage differs in effect traits. These trait groups may or may not overlap (Suding et al. 2008). In addition to the effects of single traits, trait diversity plays an important role in ecosystem functioning, even reflecting the provisioning of ecosystem services (Díaz and Cabido 2001, Díaz et al. 2007, Wellstein et al. 2011, Pappas et al. 2016). Both magnitudes and rates of ecosystem processes correlate with functional diversity, species richness and individual species abundances (Grime 1998, Díaz and Cabido 2001, Winfree et al. 2015, Craven et al. 2018). Thus, functional traits and functional diversity can help elucidate the drivers and underlying processes determining plant assemblage composition (Violle et al. 2015).

With ongoing global environmental changes, it is important to understand which drivers shape the functional composition of plant assemblages (Heilmeyer 2019). In the boreal- and Arctic regions of the Northern Hemisphere, global warming is expected to lead to increases in, for example, plant height and leaf area (Hudson et al. 2011, Pauli et al. 2012, Myers-Smith et al. 2015, Bjorkman et al. 2018b, Vuorinen et al. 2021). Precipitation can play a crucial role in shaping temperature responses (Bjorkman et al. 2018b) and in driving hydraulic traits (Griffin-Nolan et al. 2018). Past climatic conditions, such as glaciation events,

may also be of high importance to the functional composition and -diversity of present-day plant assemblages, which in turn will affect functional diversity (Ordóñez and Svenning 2015). Topographic variability and habitat heterogeneity introduce variation in plant strategies and may drive functional diversity (Hu et al. 2014, Opedal et al. 2015, Schmitt et al. 2020). Land-use changes are also known to drastically change the functionality of vegetation (Sfair et al. 2018, van der Sande et al. 2019). There is little knowledge, however, on how strongly different environmental variables affect co-variation in plant traits, and particularly how they together drive functional diversity.

Norway provides an interesting system for investigating functional biogeography. Based on the retreat of the Fennoscandian ice sheet, Norway was re-colonised relatively recently (during the last 10 000 years, after the last major ice age) and has a varied geological history (Stroeven et al. 2016). Approximately 80% of the Norwegian human population lives in densely populated areas, but < 2% and 3.5% of the Norwegian land mass consists of built-up- and agricultural areas, respectively (Statistics Norway 2020a, b). In comparison, the mean percentages for all countries in the European Union in 2018 were 70.9% of the population living in densely populated areas, 4.2% built-up area and 24.2% agricultural areas (Eurostat – Statistics Explained 2020, 2021). Norway covers more than 80% of the topological and ecological gradients of Europe as a whole (Moen 1999, Bakkestuen et al. 2008).

In this exploratory study, we aimed to investigate the geographic patterns in and drivers of functional trait distribution and -diversity of vascular plants native to Norway. To assess this, we combined vascular plant species occurrence records and compiled data on functional traits, and calculated assemblage-means for trait values of all species observed within a 20 × 20 km grid, and various measures of functional diversity. We then modelled trait assemblage-means and functional diversity indices as functions of climate- and landscape variables. We used the identified relationships to predict potential changes in functional trait distribution and -diversity for future climate projections.

Methods

Species occurrence data

We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF), using the function *occ_download* from the package *rgbif* (Chamberlain and Boettiger 2017), filtering the download to only include records with coordinates, no known geospatial issues, registered within Norway (country code=NO), and from the kingdom *Plantae* (Global Biodiversity Information Facility 2019). We further filtered the dataset to include only vascular plants native to Norway with available functional trait data. Only native species were included to focus on patterns among species which evolved in situ or migrated on their own

accord, following the species list available from Mienna et al. (2020), totalling 1421 species. As the included datasets were not all performed as strict gridded censuses, true absences could not be inferred consistently from the data. Therefore, records with 'occurrenceStatus=absent' were removed. The data were then spatially filtered to include only records occurring inside the terrestrial border of Norway (incl. a 2 km buffer), and temporally filtered to only include records from 1960 onwards. The remaining 3 783 297 species occurrence records originated from 65 different institutions, of which 48 could be classified as herbaria/museums/universities, five as state-run survey programmes, eight as professional consultants and five as citizen science programmes (Supporting information). Fifteen percent of the records were not associated with an institution code and were assumed to stem from various citizen science initiatives. Eighty-seven percent of the records were listed as 'Human observations', and 13% as living- or preserved specimens. The records were converted to a species-level presence-only grid with 20 × 20 km grid cells (WGS 84/UTM 32), following Mienna et al. (2020). Only grid cells with ≥ 100 species were included in the analyses to avoid biased trait estimates due to low species data availability.

Plant functional traits

Data on plant functional traits for the used species list was retrieved from open trait data sources. To ensure data retrieval across species synonyms, species names were standardised to match the available species names in the trait databases, using the *tnrs* function from the *taxize*-package, which utilises the Taxonomic Name Resolution Service from the iPlant Collaborative (Chamberlain and Szöcs 2013). All potential accepted synonyms were retrieved from the Integrated Taxonomic Information System and Catalogue of Life with the *synonyms*-function of the same package. The synonyms were manually checked to match the Norwegian Artsnavnebasen (Artsdatabanken [Norwegian Biodiversity Information Centre] 2015) to ensure compliance.

We requested data on functional traits from the TRY database (Kattge et al. 2019; request 4659) covering multiple leaf-, height-, seed- and chemical traits (see the Supporting information for the full list of requested traits). Additionally, we included data from Tundra Trait Team (TTT) (Bjorkman et al. 2018a) and from SeedClim (Gya 2017) to increase the coverage of tundra and Norwegian plant species. For the further analyses, we only retained traits with data for at least 70% of species observed in the grid: vegetative- and generative height (height of the highest photosynthetic- and reproductive part, respectively), leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf dry mass, seed dry mass and seed number per plant. For example, leaf N and P were excluded from the study based on these criteria. An exception was made for LDMC due to assumed importance of this trait, and as good coverage was obtained through phylogenetic inference. These traits largely capture the central functional dimensions of size, resource economics and reproduction

(Pérez-Harguindeguy et al. 2013, Díaz et al. 2016). As the compiled trait dataset included multiple measurements for each species, we calculated the mean value of each trait for each species across all datasets/measurements. Measurements with uncertain or deficient unit information were excluded to ensure data quality, and units were standardised across datasets. For nationally widespread species with missing trait data, we collected and measured specimens according to the protocol described in Pérez-Harguindeguy et al. (2013). The list of species with missing trait data was shared with skilled volunteers who collected specimens for measurements (Supporting information references: Vuorinen et al. 2020). The additional sampling of trait data provided data on generative height (data added for 43 species), vegetative height (data added for 48 species), leaf area (data added for 47 species) and leaf dry mass (data added for 50 species). These measurements were included in the calculations of average trait values for each species. In the compiled, averaged trait dataset, 77.3% of measurements originated from TRY (32% height traits, 54% leaf traits, 14% seed traits), 22.3% from TTT (47% height traits, 52% leaf traits, 2% seed traits), 0.2% from SeedClim (18% height traits, 82% leaf traits) and 0.2% from our own measurements (34% height traits, 66% leaf traits).

To fill in data gaps for species without trait values, we used the *phyEstimate*-function from the *picante*-package. This function allows predicting species trait data based on existing trait data and phylogenetic relationships between species (Kembel et al. 2010). We used a published phylogeny of the Norwegian flora (Mienna et al. 2020) and existing trait data of all vascular plants native for Norway. In addition to the eight selected traits, we determined a binary variable of woodiness for each species based on Lid and Lid (2005), as this trait may play a key role in ecosystem functioning (Weintraub and Schimel 2005, Myers-Smith et al. 2011, García Criado et al. 2020). Of the original 1260 species from the phylogeny, the following lacked data on the specified traits: 355 (28%) on vegetative height, 526 (42%) on generative height, 1037 (82%) on LDMC, 488 (39%) on leaf area, 499 (40%) on leaf dry mass, 507 (40%) on seed dry mass, 780 (62%) on seed number and 476 (38%) on SLA. Following the phylogenetic inference, the following were still inadequate: 13 (1%) lacked data on vegetative height, 13 (1%) on generative height, 24 (2%) on LDMC, 16 (1%) on leaf area, 16 (1%) on leaf dry mass, 19 (2%) on seed dry mass, 20 (2%) on seed number and 16 (1%) on SLA. Only species for which information on all traits were available or could be estimated based on the phylogenetic inference were included in the further analyses.

Based on the presence-only matrix, we used the *dbFD*-function from the *FD*-package to calculate the assemblage-mean for each trait for each cell (Laliberté et al. 2014). We calculated five metrics of functional diversity for each grid cell: species richness, functional richness, -evenness and -dispersion.

Functional richness describes the amount of functional space (convex hull volume) filled by the species of the focal assemblage. High functional richness can reflect assemblages with niche differentiation and competition (Mason et al.

2013). In general, species- and functional richness tend to be highly correlated. Functional evenness measures the evenness of abundance distribution in trait space. Functional evenness decreases if functional distance among species is irregular. Functional dispersion is the mean distance of the individual species to the centroid of the trait space occupied by all species in the assemblage (Villéger et al. 2008, Laliberte and Legendre 2010). In summary, functional richness is a measure of how much trait space is filled by an assemblage, whereas functional evenness and functional dispersion describe how this space is filled (Schleuter et al. 2010, Mason et al. 2013).

Explanatory variables for functional diversity patterns

To analyse patterns in functional diversity across Norway, we used bioclimatic variables (mean temperature of warmest quarter, annual precipitation and precipitation seasonality; downloaded from WorldClim2 (Fick and Hijmans 2017)), topographic heterogeneity (variation in altitude), habitat heterogeneity (number of land-cover categories within the grid cell), and time since last glaciation cover (time since the area was covered by the Fennoscandian ice sheet) (see the Supporting information for detailed description of the explanatory variables). A principal component analysis of the land-cover within each grid cell revealed two main axes of variation: a forest–open area gradient (PC1, explained variance of PCA = 33.38%) and an anthropogenic gradient (PC2, explained variance of PCA = 21.02%) (Supporting information). As PC1 highly correlated with temperature ($r = 0.71$), only PC2 was included as an explanatory variable. Negative values of PC2 correlated with anthropogenic land-cover types (developed area and agriculture), and positive values correlated with relatively non-anthropogenic land-cover types (forest, mire, freshwater). Therefore, PC2 can be interpreted as an inverse anthropogenic gradient. Henceforth, we will refer to this effect as ‘anthropogenic pressure’. All variables were projected (WGS 84/UTM 32), rasterised, and resampled to the 20-km grid cells.

Modelling of functional traits and -diversity.

To explore which of the predictor variables best explained patterns in trait variation, we constructed individual models predicting the unweighted assemblage mean of the five indices of functional diversity (species richness, functional richness, -evenness and -dispersion) and nine functional traits (vegetative height, LDMC, seed number per plant, SLA and woodiness, generative height, leaf area, leaf dry mass and seed dry mass). The first five of the functional traits are reported in the results. Several of the traits were highly correlated, and the ones presented in the results were deemed representative for different functional trait axes. The remaining results can be seen in the Supporting information. Specifically, vegetative height correlated highly with generative height ($r = 0.98$) and seed dry mass ($r = 0.86$), whereas SLA correlated with both leaf area ($r = 0.81$) and leaf dry mass ($r = 0.79$). Species

richness was transformed to the proportion of total number of species prior to modelling.

All models were fitted as generalised linear models, using a Gaussian distribution. To account for spatial autocorrelation, we used the Moran Eigenvector *spatial filtering* function from the packages *spatialreg* and *spdep* (Bivand and Piras 2015, Bivand and Wong 2018). As multiple models may have similar- and substantial support given the available data, one cannot confidently choose over the other solely based on log-likelihood and Akaike information criterion (AIC) values (Burnham and Anderson 2004). As a solution to this issue, we opted for multiple-model inference, in which the coefficients of the top-ranking models (based in Δ AIC) are averaged. The contribution from each of the candidate models are weighted by model support. Specifically, in this analyses ‘Akaike weights’ (normalised model likelihoods) were used as the weighting measure (Barton 2020). Additionally, multiple-model inference allowed us to estimate the relative importance and effects of the predictor variables on functional trait and -diversity patterns. We constructed a global model including all predictors for each of the response variables, using the function *dredge* in the MuMIn package (Barton 2020). All possible models from the null model to the global modal (no interactions included) were constructed and ranked based on AIC. The top-ranking models (Δ AIC < 3 compared to the best fitting model) were averaged to obtain relative variable importance and coefficient estimates (Supporting information). This threshold value for Δ AIC was based on a consistent ‘jump’ in Δ AIC values across models: when plotting Δ AIC as a function of model rank, the AIC-values sharply increased around 3, indicating a rapid decrease in model fit.

To evaluate the potential future distribution of functional traits and -diversity (in year 2081–2100), the constructed models were used to make predictions under the combination of one of the CMIP6 climate projections (MIROC6) and three Socio-economic pathways concerning greenhouse gas emissions (SSPs) (Riahi et al. 2017). As a ‘best case scenario’, we used SSP1-2.6 (van Vuuren et al. 2011), SSP2-4.5 was used as a ‘middle of the road’ scenario, and SSP5-8.5 was used as a ‘worst case/business as usual scenario’ (Riahi et al. 2011). This data was downloaded from WorldClim2 (Fick and Hijmans 2017). All other variables were kept constant and assumed not to change. The values predicted by our models given the current conditions (Supporting information) were subtracted from the future model predictions to assess the degree of change in trait and diversity metrics. We are here assuming that space can be substituted for time, which may not always be the case (Bjorkman et al. 2018b, Myers-Smith et al. 2019b). Our predictions did not take into account regional level extinctions and invasions. These results should thus be viewed solely as a theoretical exercise, and interpreted with caution.

Results

Of the initial 939 grid cells, 872 grid cells were retained for the final analyses. Excluded grid cells were primarily

along the borders of Norway, and were thus excluded based on missing data on environmental/explanatory variables (Supporting information). Of the grid cells excluded based on species data, most were located in the northernmost parts of the country. Nevertheless, a sufficient number of grid cells were retained for further analyses within this region. The final species list included 1221 species in total, which constitutes 85.9% of the native Norwegian flora.

Functional trait and -diversity patterns

Vegetative height and SLA, were positively correlated ($r > 0.7$) (Supporting information). The assemblage-mean of each of these functional traits was high along the south–west coast of Norway, typified by nemoral-, boreonemoral- and boreal vegetation, thus having a greater proportion of broadleaved tree species than the country on average (Moen 1999). In contrast, LDMC values peaked in alpine areas from south to north and in the northern regions (within the Arctic Circle) of the country, and are thus associated with climatically-harsh regions. Woodiness showed no clear distributional patterns, but had minor clusters of relatively high values in the south and north respectively, mainly associated with northern boreal regions (Fig. 1a–e).

The observed distribution of the functional diversity metrics varied, with functional richness and -dispersion being

highly correlated (Fig. 1f–i; $r=0.74$) (Supporting information). The highest species richness values were found in the southeast part of Norway along the Oslo Fjord, within the boreonemoral- and south boreonemoral zone, likely correlating with the presence of both evergreen- and broadleaf forest types. High values of functional richness and -dispersion values were seen along the west- and south coast, similarly falling within the nemoral- and boreonemoral zones. Functional evenness peaked in the northern regions of the country above the Arctic Circle and had the lowest values at the south-western coast.

Drivers of functional trait patterns

The relative importance and the effects of the different predictor variables differed for the individual trait assemblage-means (Fig. 2, Table 1, Supporting information). Be aware that while the reported results are associations, they are generally consistent with theory; we will hereafter use the term ‘affected’. Vegetative height was affected positively by precipitation, anthropogenic pressure, temperature, precipitation seasonality and topographic heterogeneity, and negatively by time since last glaciation.

LDMC was affected negatively by habitat heterogeneity, anthropogenic pressure, temperature, topographic heterogeneity and time since last glaciation. SLA was affected

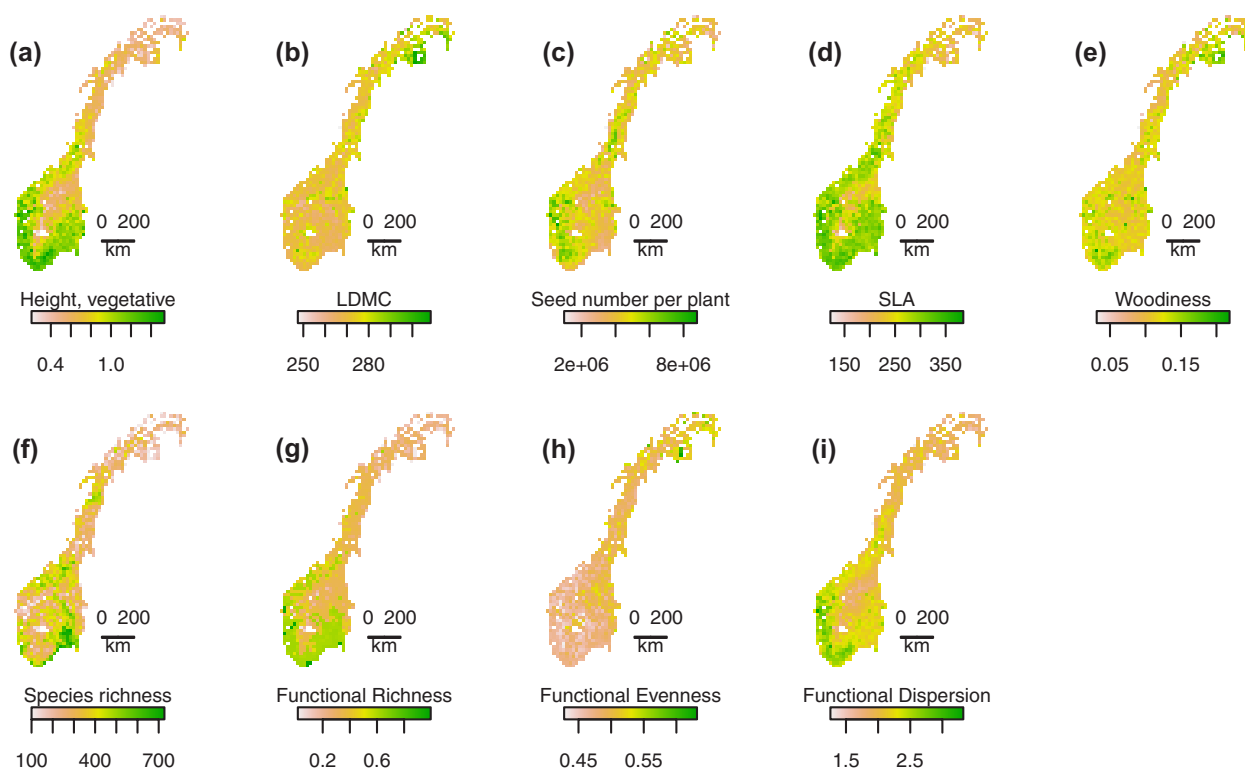


Figure 1. Observed unweighted assemblage mean (AWM) of the functional traits, based on a presence/absence matrix of 1221 native vascular plant species (a–e), and functional diversity metrics based on the species \times trait matrices for each grid cell (f–i). (a) Vegetative height (m), (b) leaf dry matter content (mg g^{-1}), (c) seed number per plant (no. seeds), (d) specific leaf area ($\text{mm}^2 \text{mg}^{-1}$), (e) woodiness (proportion of woody species), (f) species richness (no. species), (g) functional richness (convex hull volume), (h) functional evenness (evenness of abundance distribution), (i) functional dispersion (mean distance to centroid). (Projection: WGS 84/UTM 32).

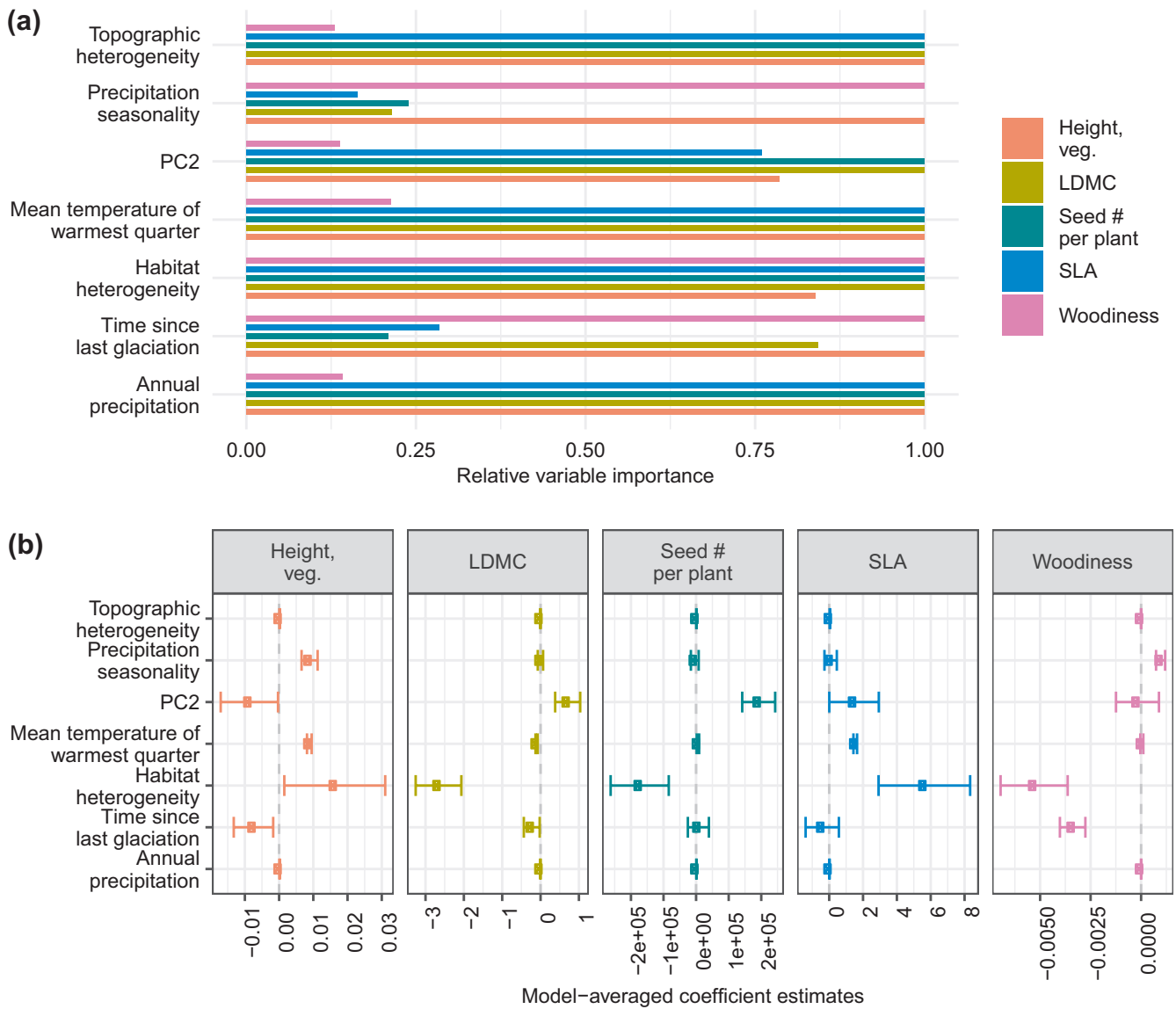


Figure 2. (a) Relative variable importance and (b) model-averaged coefficient estimates for the five functional traits. Height, veg. = vegetative height; LDMC = leaf dry matter content; seed # per plant = seed number per plant; SLA = specific leaf area; wood. = woodiness.

positively by precipitation, habitat heterogeneity, temperature and topographic heterogeneity, and negatively by anthropogenic pressure.

Seed number was affected positively by precipitation, temperature and topographic heterogeneity, and negatively by anthropogenic pressure and habitat heterogeneity. Woodiness was affected positively by precipitation seasonality, and negatively by habitat heterogeneity and time since last glaciation. Significant variables had consistently equal or almost equal variable importance.

Most important variables had an ecologically significant effect size, but the effect sizes of annual precipitation and topographic heterogeneity were consistently negligible in comparison to other variables (Fig. 2b, Table 1). Temperature had high variable importance for all traits, and topographic heterogeneity, precipitation and time since last glaciation

for most traits, but the importance of other variables varied between the traits.

Drivers of functional diversity patterns

The relative importance and the effects of the different predictor variables also differed for the functional diversity indices (Fig. 3, Table 2, Supporting information). Species richness was affected positively by habitat- and topographic heterogeneity, temperature and anthropogenic pressure, and negatively by annual precipitation. Functional richness was affected positively by annual precipitation, precipitation seasonality, temperature, anthropogenic pressure and topographic heterogeneity. Functional evenness was only affected negatively by annual precipitation, temperature, anthropogenic pressure and topographic heterogeneity. Functional

Table 1. Estimated coefficients of the averaged models of functional traits, including upper and lower 0.95 confidence intervals of the estimate. The candidate models included in the averaged model where those with $\Delta AIC < 3$ compared to the best fitting model. Coefficients for which the 0.95 CI overlaps zero are indicated with italic text. The spatial eigenvectors have not been included.

Response variable	Predictor variable	Averaged coefficient estimate	Lower 0.95 CI of coefficient estimate	Upper 0.95 CI of coefficient estimate
Height, vegetative	(Intercept)	-0.653	-0.784	-0.521
	Annual precipitation	0.0002	0.0001	0.0002
	Time since last glaciation	-0.007	-0.013	-0.002
	Habitat heterogeneity	0.016	0.002	0.031
	Mean temperature of warmest quarter	0.009	0.008	0.010
	PC2	-0.009	-0.017	-0.0003
	Precipitation seasonality	0.009	0.007	0.011
	Topographic heterogeneity	0.0002	0.0001	0.0002
SLA	(Intercept)	20.206	1.337	39.076
	Annual precipitation	0.018	0.015	0.022
	Time since last glaciation	-0.410	-1.392	0.572
	Habitat heterogeneity	5.623	2.916	8.329
	Mean temperature of warmest quarter	1.540	1.431	1.648
	PC2	1.469	0.006	2.931
	Precipitation seasonality	0.085	-0.279	0.450
	Topographic heterogeneity	0.040	0.034	0.047
LDMC	(Intercept)	307.860	303.280	312.439
	Annual precipitation	-0.003	-0.004	-0.002
	Time since last glaciation	-0.230	-0.436	-0.023
	Habitat heterogeneity	-2.661	-3.257	-2.066
	Mean temperature of warmest quarter	-0.104	-0.132	-0.075
	PC2	0.707	0.381	1.034
	Precipitation seasonality	-0.003	-0.072	0.066
	Topographic heterogeneity	-0.003	-0.004	-0.001
Seed number per plant	(Intercept)	3 199 299.157	2 609 092.943	3 789 505.372
	Annual precipitation	844.773	727.846	961.701
	Time since last glaciation	7004.553	-25 284.278	39 293.385
	Habitat heterogeneity	-173 163.196	-262 361.035	-83 965.357
	Mean temperature of warmest quarter	5594.142	1856.672	9331.612
	PC2	192 175.749	141 590.359	242 761.138
	Precipitation seasonality	-4061.170	-16 015.974	7893.635
	Topographic heterogeneity	830.714	617.717	1043.711
Woodiness	(Intercept)	0.163	0.149	0.178
	Annual precipitation	0.000001	-0.000002	0.000004
	Time since last glaciation	-0.003	-0.004	-0.003
	Habitat heterogeneity	-0.005	-0.007	-0.004
	Mean temperature of warmest quarter	0.00004	-0.00004	0.00011
	PC2	-0.0002	-0.0012	0.0009
	Precipitation seasonality	0.0010	0.0007	0.0012
	Topographic heterogeneity	0.000000	-0.000004	0.000004

dispersion was affected positively by annual precipitation, temperature, precipitation seasonality and topographic heterogeneity, and negatively by time since last glaciation. Statistically significant variables had consistently equal or almost equal variable importance.

Similar to the individual traits, the effect sizes of annual precipitation and topographic heterogeneity were negligible, though statistically significant (Fig. 3b, Table 2). Annual precipitation, temperature and topographic heterogeneity had high variable importance for all indices, but the importance of other variables varied between the indices.

Future projections

The direction of change in assemblage-means of functional traits were similar for all three climate/SSP scenarios (Fig. 4, Supporting information). Height and SLA are predicted to increase across the country, particularly in coastal areas and in the northern regions. In contrast, LDMC is generally predicted to decrease across the country. Seed number per plant are predicted to increase in most of the country, with a decrease around mid-Norway, coinciding somewhat with the Arctic Circle. Woodiness mainly increased, particularly along the

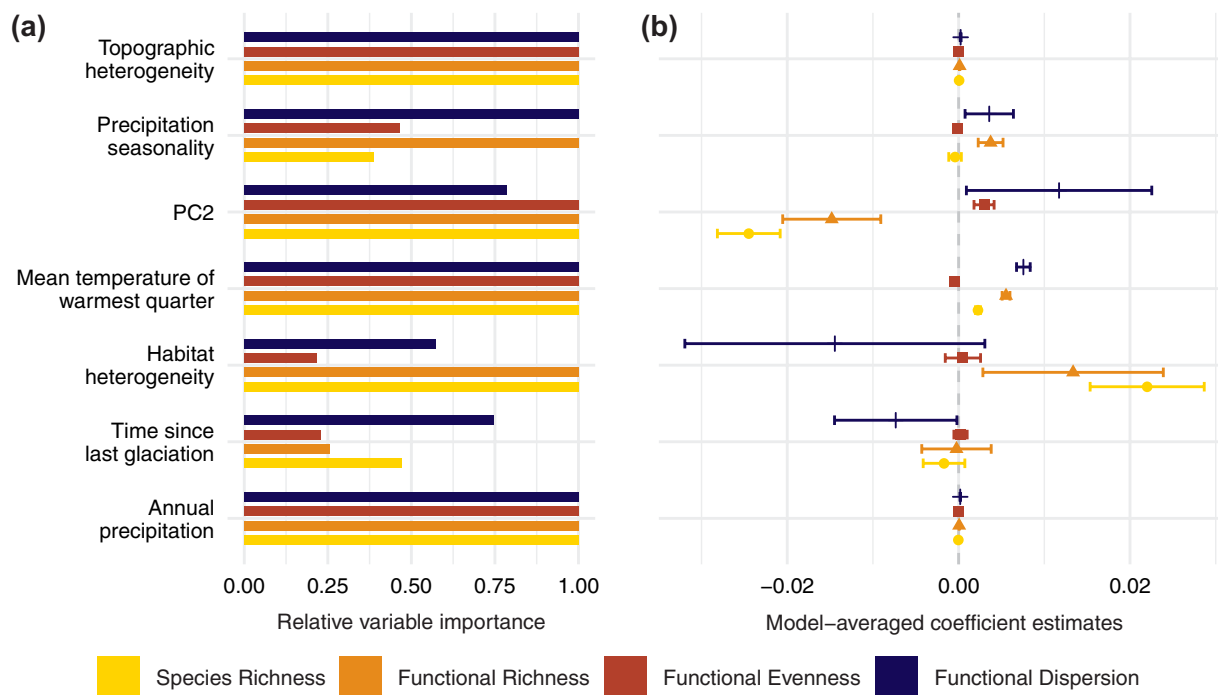


Figure 3. (a) Relative variable importance and (b) model-averaged coefficient estimates for the four (functional) diversity metrics.

coast and in northern inland regions (the arctic and subarctic tundra in Finnmark). It decreased, however, in the southern inland/southern boreal zone and along the coast in the north. The extent of changes were much larger in the ‘worst case scenario’ compared to the ‘best case scenario’, with the ‘middle of the road’ scenario falling in between the two extremes.

Likewise, the qualitative results for the projections of functional diversity indices were similar, though they differed in extent (Fig. 4, Supporting information). Species richness, functional richness and -dispersion generally increased across Norway. Species- and functional richness increased the most in coastal- and northern regions, functional dispersion showed the greatest increases in northern regions and along the south- and west coast. The projections of functional evenness decreased across the country.

Discussion

In this paper, we investigated the patterns and drivers of functional traits and -diversity across a northern region of Europe. We found that climate and land-use both shape plant functional composition, highlighting the importance of multiple environmental factors in driving plant functional traits and -diversity in time and space. Given projected future climate change, our models predict species- and functional richness of the Norwegian flora to increase, but also to shift towards tall, woody, fast-growing species.

Patterns and drivers of functional traits

Plant traits in northern ecosystems are shaped by climate (Bjorkman et al. 2018b), and global warming changes the

functionality of temperate, boreal and alpine vegetation (Parmesan 2006, Walker et al. 2006, Hudson et al. 2011, Reu et al. 2011, Hedwall and Brunet 2016, Stewart et al. 2018, Myers-Smith et al. 2019b). Our results corroborate these findings by showing that temperature plays a crucial role for spatial patterns of the assemblage-means of all studied traits, and by predicting climate-driven changes in most of them (Fig. 2, 4, Table 1). Assemblage-means of traits related to plant size and growth speed (height, SLA) were highest in warm areas (Fig. 1), and we predicted future increases (Fig. 4, Supporting information), in agreement with plant trait studies covering the whole tundra biome (Hudson et al. 2011, Bjorkman et al. 2018b). Woodiness is predicted to increase in the future, likely reflecting the increasing shrub and tree abundance expected in northern and high-altitude regions; the shrubification of the Arctic (Harsch et al. 2009, Myers-Smith et al. 2011, 2019b, Myers-Smith and Hik 2018, García Criado et al. 2020). In contrast, LDMC responds negatively to summer temperature and is predicted to decrease. The future flora of Norway will likely include species with faster growth strategies and a somewhat elevated proportion of woody species. Our study did not include abundances of the individual species, only presence. However, should these changes in traits of the species present also reflect changes in abundances, this increase in woody plants can cause a shift in overall ecosystem composition and functioning (Myers-Smith et al. 2019b, García Criado et al. 2020). Shrubification and/or forest advancement may increase vegetation closedness and carbon storages, decrease albedo, enhance plant-plant competition and soil nutrient cycling, and modify hydrology and decomposition (Lavorel and Garnier 2002, Walker et al. 2006, Cornwell et al. 2008, Gottfried et al.

Table 2. Estimated coefficients of the averaged models of functional diversity indices, including upper and lower 0.95 confidence intervals of the estimate. The candidate models included in the averaged model were those with $\Delta AIC < 3$ compared to the best fitting model. Coefficients for which the 0.95 CI overlaps zero are indicated with italic text. The spatial eigenvectors have not been included.

Response variable	Predictor variable	Averaged coefficient estimate	Lower 0.95 CI of coefficient estimate	Upper 0.95 CI of coefficient estimate
Species richness	(Intercept)	-0.099	-0.153	-0.045
	Annual precipitation	-0.00003	-0.00004	-0.00002
	Time since last glaciation	-0.002	-0.004	0.001
	Habitat heterogeneity	0.022	0.015	0.029
	Mean temperature of warmest quarter	0.0023	0.0020	0.0026
	PC2	-0.024	-0.028	-0.021
	Precipitation seasonality	-0.0004	-0.0012	0.0003
	Topographic heterogeneity	0.00006	0.00004	0.00008
Functional richness	(Intercept)	-0.519	-0.596	-0.442
	Annual precipitation	0.00006	0.00005	0.00008
	Time since last glaciation	0.000	-0.004	0.004
	Habitat heterogeneity	0.013	0.003	0.024
	Mean temperature of warmest quarter	0.0055	0.0051	0.0060
	PC2	-0.015	-0.021	-0.009
	Precipitation seasonality	0.004	0.002	0.005
	Topographic heterogeneity	0.00012	0.00009	0.00015
Functional evenness	(Intercept)	0.582	0.569	0.596
	Annual precipitation	-0.000015	-0.000018	-0.000012
	Time since last glaciation	0.000	-0.001	0.001
	Habitat heterogeneity	0.001	-0.002	0.003
	Mean temperature of warmest quarter	-0.0005	-0.0006	-0.0004
	PC2	0.003	0.002	0.004
	Precipitation seasonality	-0.0002	-0.0005	0.0001
	Topographic heterogeneity	-0.000027	-0.000031	-0.000023
Functional dispersion	(Intercept)	0.964	0.784	1.143
	Annual precipitation	0.00019	0.00016	0.00021
	Time since last glaciation	-0.007	-0.014	-0.0002
	Habitat heterogeneity	-0.014	-0.032	0.003
	Mean temperature of warmest quarter	0.0076	0.0068	0.0084
	PC2	0.012	0.001	0.023
	Precipitation seasonality	0.004	0.001	0.006
	Topographic heterogeneity	0.00024	0.00019	0.00029

2012, Bjorkman et al. 2018b, Stewart et al. 2018, Myers-Smith et al. 2019b, Vuorinen et al. 2021).

Even though precipitation plays a role in the functional composition of the Norwegian flora, its effect size is minor in comparison to temperature (Fig. 2b, Table 1). This contrast the study by Moles et al. (2009), who found precipitation to be more important than (winter) temperature for the variation in plant height globally. They did nevertheless point out that the opposite might be case in cold regions, which our results support. Other studies highlight the importance of precipitation and water availability (Griffin-Nolan et al. 2018), but rather than precipitation per se, the timing of rain can be crucial for the functional composition of plant assemblages (Swenson et al. 2012, Moles et al. 2014). Many of the included functional traits are part of the leaf economic spectrum. These have been suggested to be unreliable within the context of water availability (Griffin-Nolan et al. 2018). Unexplored traits, such as hydraulic traits, might have shown responses better related to precipitation (Moles et al. 2014).

In addition to current and future climate, plant traits are affected by glacial history: height, LDMC and woodiness decreased with time since last glaciation (Fig. 2b, Table

1). Notably, time since last glaciation is highly correlated with distance to the coast (Supporting information), as the Fennoscandian ice sheet retreated from the coast to inland and alpine areas (Stroeven et al. 2016). Thus, this variable also reflects a coastal-inland gradient, with high values reflecting coastal areas. The variation in functional diversity along this gradient can likely be attributed to variation in other environmental variables (such as oceanic versus inland climate) rather than to evolutionary history.

As for the local effects, habitat heterogeneity decreases woodiness and LDMC and increases SLA. Anthropogenic pressure, on the other hand, increases vegetative height (Palma et al. 2017), but decreases LDMC (Knapp et al. 2008, Kalusová et al. 2017), SLA and seed number per plant (Fig. 2b, Table 1). This relationship potentially stem from the fact that anthropogenic- and agricultural areas have generally been established in productive environments (Gaston 2005), where these traits are more frequent – the relationship is thus more associational than causal. Topographic heterogeneity appears important in driving all studied traits. Yet, its effect sizes are too modest to match those of climatic factors.

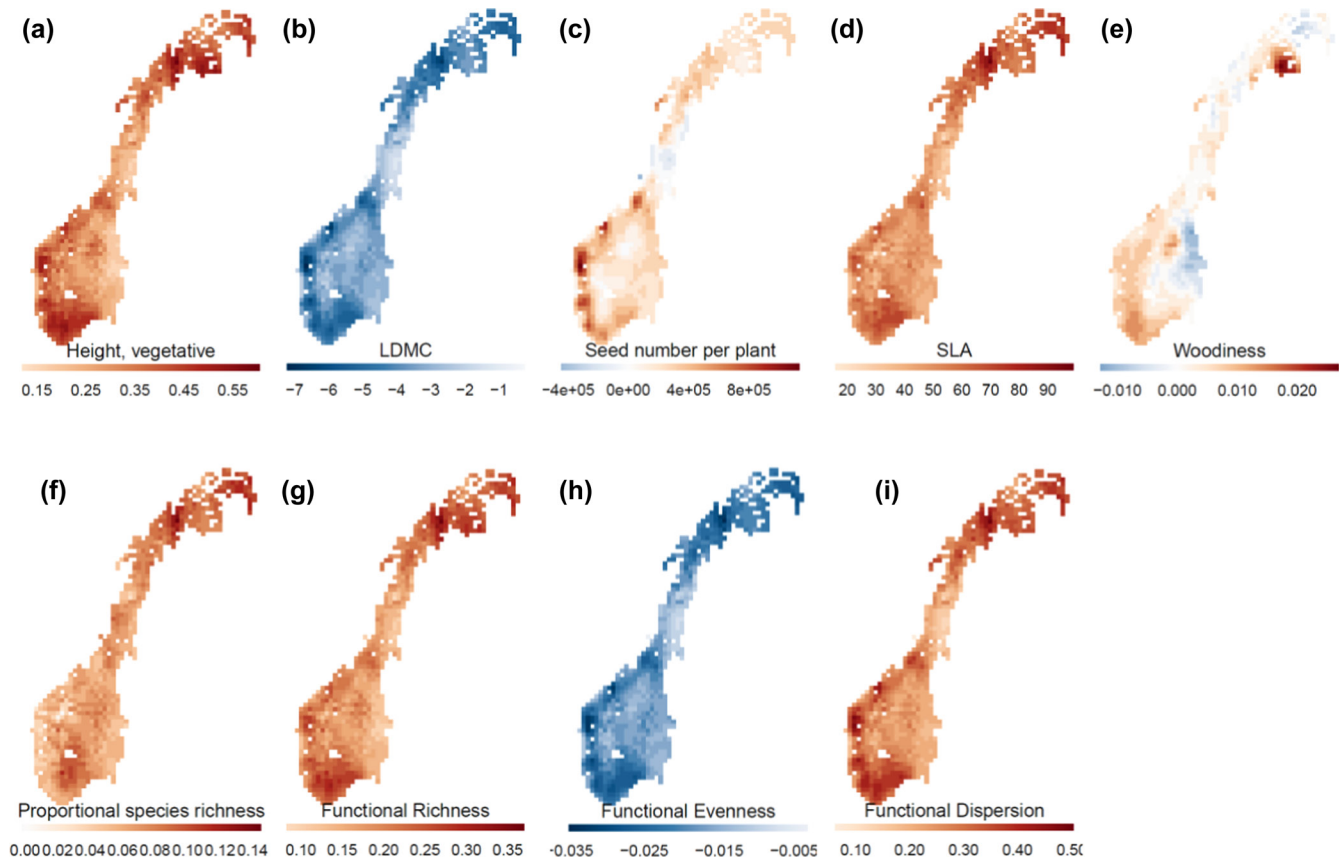


Figure 4. Change in unweighted assemblage mean of the functional traits (a–i) and functional diversity metrics (j–m) in 2081–2100 based on projected climate change (CMIP6, MIROC6) given the ‘middle of the road’ scenario (SSP2-4.5). (a) Vegetative height (m), (b) leaf dry matter content (mg g^{-1}), (c) seed number per plant (no. seeds), (d) specific leaf area ($\text{mm}^2 \text{mg}^{-1}$), (e) woodiness (proportion of woody species), (f) relative species richness (compared to total species richness), (g) functional richness (convex hull volume), (h) functional evenness (evenness of abundance distribution), (i) functional dispersion (mean distance to centroid). (Projection: WGS 84/UTM 32).

In the projections reported here, only bioclimatic variables are assumed to change. This is a highly unrealistic scenario, as, for example, projections of land-use change in Norway predicts a substantial increase in built-up- and agricultural areas at the expense of, for example, forests and wetlands (Søgaard et al. 2019). This could further affect the effects of climate changes, either through exacerbation or by counteracting them (Sfair et al. 2018, Dalle Fratte et al. 2019).

This study reported five functional traits, all concerning aboveground characteristics. van der Plas et al. (2020) showed that studies of plant functional traits, as predictors of ecosystem functioning, have generally neglected belowground traits, despite their importance for ecosystem functioning (Myers-Smith et al. 2019b). Data availability limited the inclusion of additional traits, and analysis of the suitability of functional traits or -diversity as predictors of ecosystem functioning was not the aim of this study. The traits included here are generally considered relevant as they are considered central to the plant life cycle (Pérez-Harguindeguy et al. 2013).

Patterns and drivers of functional diversity indices

The positive effects of summer temperature on species richness (Fig. 3b, Table 2) are in concordance with the general latitudinal gradient in species diversity (Gaston 2000, Willig et al. 2003). The positive effect of habitat heterogeneity was also seen by Mienna et al. (2020), as it is associated with variation in environmental conditions, allowing for niche partitioning. The observed positive effect of anthropogenic pressure on species richness is not necessarily a causal relationship. Previous studies have shown that species occurrence records are biased towards areas with high population densities or anthropogenic land-uses in Norway (Speed et al. 2018, Petersen et al. 2021), demonstrating an effect of sampling effort. This relationship is potentially complex as urban- and agricultural land have frequently been placed in productive areas with high biological diversity (Gaston 2005). In contrast to the findings of Mienna et al. (2020), time since last glaciation is not found to be a highly important variable for species richness. This discrepancy can likely be attributed to the differences in the used datasets. Despite similar number of species (1221 species versus 1235

species), the number of included grid cells differ due to trait data availability (872 versus 1041 grid cells). A potential solution to this issue could be to use rarefaction to get a measure of likely species richness in all grid cells. This would however only provide data on species richness, and not on other functional diversity indices or individual functional traits.

As functional richness and species richness are somewhat correlated (Supporting information), many of the interpretations and explanations described for species richness are transferable to functional richness. This is particularly the case for the effects of temperature and anthropogenic pressure. Likewise, functional richness and -dispersion correlate enough to warrant similar interpretations. These three indices increase towards warm and topographically heterogeneous regions. Functional richness and -dispersion increase with precipitation and functional dispersion increases with increasing precipitation seasonality. The three indices peak along the south- and west coast (Fig. 1). Relatively few trait syndromes seemingly dominate these assemblages with stressful abiotic conditions (Hesp 1991, Nylén and Luoto 2015). The lowest functional diversity indices are seen in alpine areas.

Functional evenness generally decreases towards warm, wet and topographically varied regions, and areas with high anthropogenic pressure, peaking in northern Norway (Fig. 1). The negative effect of anthropogenic pressure on this index reflects that species are irregularly distributed in trait space.

Predictions of functional diversity, given future climate projections, indicate that species richness, functional richness and -dispersion will increase across the country. Functional evenness will decrease, depending on the severity of climate change (Fig. 4, Supporting information). This is in concordance with Reu et al. (2011), who found increasing functional richness at mid-high latitudes with climate change. Increasing species- and functional richness suggest future immigration of functionally different species. The simultaneous increase and decrease in respectively functional richness and -evenness show that, though the functional range of plant species within assemblages will increase, this expansion will not happen uniformly. Rather, certain trait combinations will be favoured (Díaz et al. 2016).

It is important to note that our models and projections have not taken into account intraspecific trait variations, abundances or biotic interactions. These might affect species' abilities to manage changing environments (Moran et al. 2016) and assembly processes (Bruehlheide et al. 2018), and are worthy of further investigation at large spatial scales.

Conclusion

In this study, we show that geographic variation in assemblage-means of functional traits and diversity of vascular plants can be predicted by climate, landscape and history, and future environmental changes will influence the functional composition of the Norwegian flora. Climatic variables are the main drivers of functional diversity, with a positive effect of increasing temperatures on functional diversity.

The global climate is changing rapidly with increasing temperatures in the northern regions, as is anthropogenic land-cover types and land-use intensity (Jia et al. 2019), all affecting the future of global plant diversity (van Vuuren et al. 2011). Several studies have pointed to the expected effects of future climate- and land-cover change on vascular plant diversity in alpine, arctic and boreal regions, such as altitudinal distribution shifts (Lenoir et al. 2008, Pauli et al. 2012, Steinbauer et al. 2018), homogenisation of arctic assemblages (Stewart et al. 2018) and shifts in phylogenetic composition (Mienna et al. 2020). Our study illustrates that shifts in functional composition of assemblages will accompany increases in temperature. Species will be taller and have larger leaves. Furthermore, a greater proportion of species will be woody, corroborating the shrubification- and treeline shift trends of the northern biomes (Myers-Smith et al. 2019a, García Criado et al. 2020, Mekonnen et al. 2021). Despite increasing functional richness across the country, certain trait combinations will be favoured.

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Author contributions

Tanja K. Petersen and **Katariina E. M. Vuorinen** contributed equally to this publication. **Tanja K. Petersen:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Katariina E. M. Vuorinen:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Mika Bendiksbj:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **James D. M. Speed:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Species occurrence records are available from public repository (GBIF Occurrence Download – 20 Feb 2019, <<https://doi.org/10.15468/dl.sxzechz>>).

Supporting information

The Supporting information associated with this article is available with the online version.

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