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Differential patterns of floristic phylogenetic diversity across a post-glacial landscape

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Abstract

Aim: In this study, we explored spatial patterns of phylogenetic diversity (PD) and endemism in the flora of Norway and tested hypothesized post-glacial environmental drivers of PD, including temperature, precipitation, edaphic factors and time since glacial retreat.

Location: Norway.

Taxon: Vascular plants (Trachaeophyta).

Methods: We produced a multi-locus maximum-likelihood (ML) phylogeny using a combination of newly produced DNA sequences from herbarium specimens and sequences available from public repositories. We combined the phylogeny with species occurrence data to estimate PD and phylogenetic endemism across Norway, using a spatial randomization to judge statistical significance. We used multiple-model inference to identify environmental variables that contributed the most to the patterns of PD. Finally, we estimated phylogenetic turnover and used this to identify Norwegian plant assemblages in terms of composition and evolutionary history.

Results: Our ML phylogeny contained 87% of all currently described native Norwegian vascular plants. Assemblages were phylogenetically overdispersed in warmer and wetter regions of Norway, as well as in regions with a longer post-glacial history. In cold and dry regions, plant assemblages were phylogenetically clustered, and characterized by neo-endemism, while the mild and wet regions were characterized by both paleo- and neo-endemism. PD was positively correlated with summer temperature and habitat heterogeneity, and peaked in the southeast of Norway.

Main conclusions: Both contemporary ecological factors (climate and habitat heterogeneity), and post-glacial history seem to have shaped the phylogenetic structure of the flora of Norway. The flora in the far north of Norway appear to be a result of recent diversification while the coastal regions are assemblages of deeper lineages. Our results suggest that there is an evolutionary signal in the distribution of the Norwegian vascular flora.

KEYWORDS

flora, Norway, nunatak, phylogenetic diversity, phylogenetic endemism, post-glacial, spatial phylogenetics, species richness, vascular plants

1 | INTRODUCTION

Understanding observed biodiversity patterns is important for conservation issues. While species-level biodiversity patterns are most commonly studied in conservation biology, some regard phylogenetic diversity (PD) to be of greater importance since it encompasses the evolutionary history of the species (Faith, 1992; Kling, Mishler, Thornhill, Baldwin, & Ackerly, 2019). Spatial phylogenetics combines species occurrence data with molecular phylogenetics to recover information about the spatial distribution of PD and phylogenetic endemism (PE) across selected geographical regions (Mishler et al., 2014; Thornhill et al., 2016). This approach makes it possible to discover centres of endemism, distinguish phylogenetically clustered communities from phylogenetically dispersed ones and identify regions differing in phylogenetic composition. Such information is of both ecological and conservational interest.

Previous studies have investigated spatial patterns of PD and endemism of vascular plants in regions with long evolutionary histories, such as Australia (Mishler et al., 2014; Nagalingum et al., 2015; Thornhill et al., 2016), Chile (Scherson et al., 2017), California (Thornhill et al., 2017), Mexico (Sosa, De-Nova, & Vasquez-Cruz, 2018) and Florida (Allen, Brown, & Gillooly, 2002). In these regions, the flora has had considerable opportunity to evolve in situ. A recent study of the flora in Wisconsin looked at PD in a recently glaciated area where they found PD to change with latitude (Spalink et al., 2018). However, what drives PD and endemism patterns in younger floras, for example those with a limited post-glacial existence, needs more study. In floras with a short evolutionary history, regardless of the cause, it is likely that immigration plays a larger role in determining the phylogenetic composition of communities than in situ diversification (Ma, Sandel, & Svenning, 2016).

Norway is a biogeographically interesting region for multiple reasons. First, Norway was covered by the Fennoscandian Ice Sheet 22–9.7 thousand years ago (kyr BP; Stroeven et al., 2016). Plants and animals now inhabiting Norway are therefore most likely recent immigrants from areas such as southern and eastern Europe (Hewitt, 1999; Nordal, Jonsell, & Marcussen, 2005). Some studies have, however, argued for glacial survival of plants on the so-called *nunataks* rising above the ice sheet (see e.g. Parducci et al., 2012; Westergaard et al., 2011). Second, Norway contains a wide variation in topography and climate. The landscape of Norway was shaped by the Fennoscandian Ice sheet and is presently represented by deep fjords and steep mountains that affect Norway's climatic conditions. The mean annual temperature changes with both elevation (from 0 to 2,469 m a.s.l.) and latitude (57°N to 71°N) and ranges from −6 to + 7°C (Moen, 1999). Norway has a strong precipitation gradient varying with high precipitation levels in the west and low levels in the east (4°E to 31°E). All vegetation zones recognized in Northern Europe can be found in Norway: alpine, boreal (northern, middle and southern), boreonemoral and nemoral zone (Moen, 1999). The geology of Norway is complex but mainly consists of acidic basement rocks like gneiss and granite and bedrock affected by the Caledonian orogeny giving calcareous-rich soil. Third, while Norway is not regarded as a hotspot for vascular plant diversity and endemism, it does host multiple vascular plants considered as priority species for conservation in Europe (Henriksen & Hilmo, 2015). Fourth, the national Norwegian herbarium collections of vascular plants are near to completely digitized, with over five million occurrences directly available via the Global Biodiversity Information Facility (GBIF.org), enabling the use of recently developed methods to study PD patterns of the entire vascular flora of Norway.

In this study, our objectives were to estimate patterns of PD and endemism in vascular plants native to Norway and to identify potential drivers of these patterns. In addition, we aimed to distinguish and compare plant assemblages across Norway in terms of their species composition and evolutionary history. Abiotic factors like temperature and precipitation are primary drivers of species distributions as they influence the niche of a species (Holt, 2009; Hutchinson, 1957). Earlier studies using spatial phylogenetics found closely related vascular plant species in Australia co-occurring (i.e. phylogenetic clustering) in areas with high temperature and low precipitation (Thornhill et al., 2017, 2016). These conditions are thought to be stressful for plants and closely related species may share traits because of niche conservatism (Wiens & Graham, 2005). Using a different approach, Grytnes, Birks, Heegaard, and Peglar (2000)found phylogenetic clustering of vascular plants in northern Fennoscandia and at high elevations in southern Fennoscandia. Therefore, we predicted (*P1*) that regions with low temperature and precipitation (i.e. stressful conditions for plants) would have phylogenetically clustered communities. Temperature and annual precipitation, and spatial heterogeneity in habitats, topography and soil pH have all been shown to be strong predictors of plant richness (Bruun et al., 2006; Kreft & Jetz, 2007; Pärtel, 2002). Thus, we predicted (*P2*) that these factors are positively related to both vascular plant species richness (SR) and PD in Norway. The number of vascular plants in Norway is increasing over the Holocene (Felde, Grytnes, Bjune, Peglar, & Birks, 2017). We therefore predicted (*P3*) that SR and PD both are positively correlated with time since the area was last covered by ice. Categorizing endemism in relation to their phylogenetic branch lengths may give different results. Paleo-endemism (range-restricted, long phylogenetic branches) has been proposed to be located in areas with long evolutionary history, while neo-endemism (range-restricted, short phylogenetic branches) can be found close to areas with recent diversification (Mishler et al., 2014). We therefore predicted (*P4*) that paleo-endemism will peak close to potential immigration routes or nunataks (if those existed) and neo-endemism will peak in any centres of recent diversification.

2 | MATERIALS AND METHODS

2.1 | Species selection

A list of vascular plant species occurring in Norway was obtained from The Norwegian Biodiversity Information Centre (Table B1 in

Supplementary information 2). Only species native to Norway were used. We obtained the information concerning native status from Lid and Lid (2005), who define native species as those that have come to an area without the aid of humans. The goal was to have each terminal node in the phylogeny represent a single species (Table B2 in Supplementary information 3). This preliminary list of 1,421 species was filtered according to criteria detailed below.

2.2 | Species occurrence data

We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF) using the function *name_backbone* in the R package *rgbif* (Chamberlain, Ram, Barve, & Mcglinn, 2017; R Core Team, 2017) in November 2017 (GBIF.org, 2017). Species were excluded from the study if they had no recorded *species key* using the function *name_backbone*, had less than two occurrences, had only occurrences older than the year 1900 or had only occurrences labelled 'doubtful'. For taxa that Lid and Lid (2005) or The Norwegian Biodiversity Information Centre (Table B1 in Supplementary information 2) defined as a species, but GBIF defined as a synonym, hybrid or subspecies, we instead used a *usage key* to collect occurrences. We obtained both occurrence records stated as human observations and those with accompanying preserved specimens. While earlier spatial phylogenetics studies relied on occurrence data solely from preserved specimens (Mishler et al., 2014; Scherson et al., 2017; Thornhill et al., 2017), we chose to include human observations to maximize potential coverage of the species' distributional ranges, and account for differential spatial, taxonomic and environmental biases between the record types (Speed et al., 2018). Occurrences outside of the Norwegian border were removed, as were records with spatial uncertainty >2 km. Following the previously outlined processes, the data were used 'as is'. The reasoning for this was that the majority of the records were published by reputable organizations (such as the Norwegian Botanical Society and the University Museums and herbaria); therefore, we expect identification errors to be low. In total, 3,597,865 occurrences were converted into a species-level presence–absence grid with 1,094 20 × 20 km grid cells (WGS 84/UTM zone 32N). A 20 × 20 km resolution was selected as the estimated optimum trade-off between spatial precision and completeness across the whole of Norway (see also Baldwin et al., 2017).

To ensure that spatial analyses of diversity were limited to well-sampled regions, the data were tested for completeness (Chao, 1987). For the completeness testing, the expected number of species in a cell was calculated using the function *estimateR* from the R package *vegan* (Oksanen et al., 2017). Completeness was calculated by dividing observed species occurrence number in a cell by expected species number; 53 cells had a completeness <50% and so were removed from the dataset. As *Chamaedaphne calyculata* only occurred in cells with low completeness, it was removed from analyses. After this filtering, 1,238 species remained in the final species list.

2.3 | Sequence alignment and phylogeny

We used MATRIX MAKER (Freyman & Thornhill, 2016) in combination with manual searching to mine GenBank (Benson et al., 2013) and BOLDSYSTEMS (Ratnasingham & Hebert, 2007) for ITS, *mat*K and *rbc*L sequences for the filtered list of species. We used MAFFT 7 (Katoh & Standley, 2013) to perform automated alignments of the GenBank/BOLD sequences and our 196 newly generated sequences (Supplementary materials and methods section 'Molecular data' and Table A1 in Supplementary information 1). The three single-locus alignments were concatenated into a multiple sequence alignment (MSA). A maximum-likelihood analysis of the MSA was performed using RAxML (Stamatakis, 2006) under the GTRGAMMA nucleotide substitution model and a separate data partition for each of the three loci. The topology of the resulting tree was verified by comparing it to the work of the Angiosperm Phylogeny Group IV (APG IV) (Byng et al., 2016). Alignment corrections were performed if species were misplaced according to APG IV. If a genus was non-monophyletic, and corrections of the alignment did not help, species in the genus were included anyway. Poorly supported branches (<70%) were examined. If alignment corrections did not remove the low support, but the placement of the taxa was correct according to the APG IV system, the branch was not inspected any further. The monophyletic pteridophyte clade was chosen as the outgroup of the phylogeny (Bateman, Hilton, & Rudall, 2006). The MSA used to generate the final phylogeny contained 1,238 species (87% of the total number of vascular plant species native to Norway) (File X1 in Supplementary information 1).

We used a *phylogram* for the analyses presented here, that is, the branch lengths were expressed in units of inferred mutations. This is common in spatial phylogenetic analyses, but it can also be useful to time-calibrate the tree and use a *chronogram* to infer phylogenetic metrics. Recent studies (Allen et al., 2019; Thornhill et al., 2017) compared the results of using a phylogram versus a chronogram, showing that there can be differences in results of the spatial randomizations. One approach is not better than the other—these two approaches to estimate branch lengths represent different facets of phylodiversity, as discussed in detail by Kling et al. (2019). The phylogram infers the distribution of evolutionary character change on the map, whereas the chronogram infers the distribution of elapsed evolutionary time. The use of one or the other approach depends on the investigator's goals. We chose to use a phylogram here for two reasons: (a) we wanted to emphasize the genetic change facet of PD and see how it correlates with potential environmental drivers; and (b) the phylogram has fewer assumptions in that the chronogram starts with the same inferred genetic change but contracts and lengthens branch lengths to make the tree ultrametric according to added assumptions about ages. The phylogram is therefore a more straightforward representation of the data, in this case.

2.4 | Spatial phylogenetic analyses

Biodiverse 1.99_088 (Laffan, Lubarsky, & Rosauer, 2010) was used to combine the spatial data and phylogeny. The following indices

were estimated using a *Biodiverse* automation pipeline (github.com/NunzioKnerr/biodiverse_pipeline), following the methods in Mishler et al. (2014) and Thornhill et al. (2016): SR, PD, weighted endemism (WE), PE, relative phylogenetic diversity (RPD) and relative phylogenetic endemism (RPE). Spatial randomizations of PD, PE, RPD and RPE were performed using the *rand_structured* option in *Biodiverse* wherein species are randomly reassigned to the map with two constraints, richness in each grid cell and range size of each species are held constant. This randomization allows discovery of areas with phylogenetic clustering or overdispersion and areas with concentrations of short or long range-restricted branches (Laffan & Crisp, 2003; Mishler et al., 2014). A categorical analysis of neo- and paleo-endemism (CANAPE) was performed to identify statistically significant concentrations of high PE, and determine whether they are dominated by either paleo-endemism (range-restricted, long phylogenetic branches) or neo-endemism (range-restricted, short phylogenetic branches) as described in Mishler et al. (2014) and Thornhill et al. (2016).

In addition to these alpha diversity metrics, we also studied beta diversity. We used a recently proposed alternative to normal turnover metrics that upweights range-restricted taxa (or branches in the phylogenetic case; Laffan et al., 2016). We calculated range-weighted species turnover (RWTurnover) and range-weighted phylogenetic turnover (PhyloRWTurnover) using *Biodiverse* to identify regions containing similar species or similar branches of the phylogeny, respectively. The regions of similarity discovered here were then compared to previously published hypotheses about Norway's vegetation from the literature (Moen, 1999).

2.5 | Assembly of explanatory variables for diversity and endemism patterns

We used seven potentially explanatory variables to analyse the diversity and endemism patterns. These were as follows: three bioclimatic variables (annual precipitation, mean temperature of warmest quarter (henceforth called summer temperature) and precipitation seasonality), habitat heterogeneity (number of habitat classes found in each cell), soil pH, time since last glaciation cover (time since area was covered by the Fennoscandian ice sheet) and topographic heterogeneity (variation in altitude) (see Table A2 and Figure A1 in Supplementary information 1 for more information regarding the selection and sources of environmental variables). The three bioclimatic variables were chosen for this study as they have previously been found to explain 89% of the bioclimatic variation in Norway (Speed & Austrheim, 2017). All variables were projected to WGS 84/UTM zone 32 N and then rasterized and resampled to 20-km grid cells.

2.6 | Modelling of diversity patterns

Four diversity metrics, observed SR, observed PD, significantly high PD (henceforth referred to as phylogenetic overdispersion) and significantly low PD (henceforth referred to as phylogenetic clustering), were statistically modelled to find which explanatory variables could best predict the four diversity patterns. Phylogenetic clustering (concentrations of closely related species) and overdispersion (concentrations of distantly related species) were derived from the randomized PD results, and divided into two binomial datasets before modelling. Possible correlations between all variables (response and explanatory) were investigated (Figure A2 in Supplementary information 1). The maximum correlation coefficient was found between SR and observed PD (0.97). For the explanatory variables, a threshold of 0.7 was chosen but no pairs of explanatory variables exceeded this threshold as the maximum correlation coefficients were found between summer temperature and pH, and summer temperature and topographic heterogeneity (0.49).

We fitted all models as generalized linear models. For SR and PD, the Gaussian distribution was chosen as the distribution model, and high and low PD as binomial (high PD vs. non-high PD and low PD vs. non-low PD). To account for the spatial autocorrelation between the data, we used the Moran Eigenvector spatial filtering function from the package *spdep* (Bivand & Piras, 2015). The function removes the spatial autocorrelation in the residuals by selecting eigenvectors (Griffith, 2000) as explanatory variables in the model until the residuals fall below a specified tolerance level (Wang, Kockelman, & Wang, 2013).

We used multiple-model inference to estimate the relative effect of the environmental variables on diversity patterns. We used the function *dredge* from the package *MuMIn* (Barton, 2018) in R to calculate the Akaike information criteria (AIC) value of all possible models from the null model to one including all univariate variables. Model averaging was used to infer the relative importance of the explanatory variables for the four diversity patterns by giving the models with lowest AIC value more weight than models with higher AIC values. Coefficient estimates for the different explanatory variables were averaged and weighted by model importance across the models where the variable was present (see Table A3 in Supplementary information 1 for top-ranked models). Due to missing values for topographic heterogeneity, soil pH and the three bioclimatic variables, 45 grid cells were removed from the statistical analyses.

3 | RESULTS

3.1 | Spatial and molecular data

The final spatial dataset contained 3,583,709 records in 1,041 20 km × 20 km grid cells (File X2 in Supplementary information 1). The final phylogeny for 1,238 species generally had high support, and all families and orders were monophyletic (Figure A3 and File X3 in Supplementary information 1).

3.2 | Diversity patterns and drivers

The observed distribution patterns of SR and PD were very similar (Figure 1a,b; r = .97 Figure A2 in Supplementary information

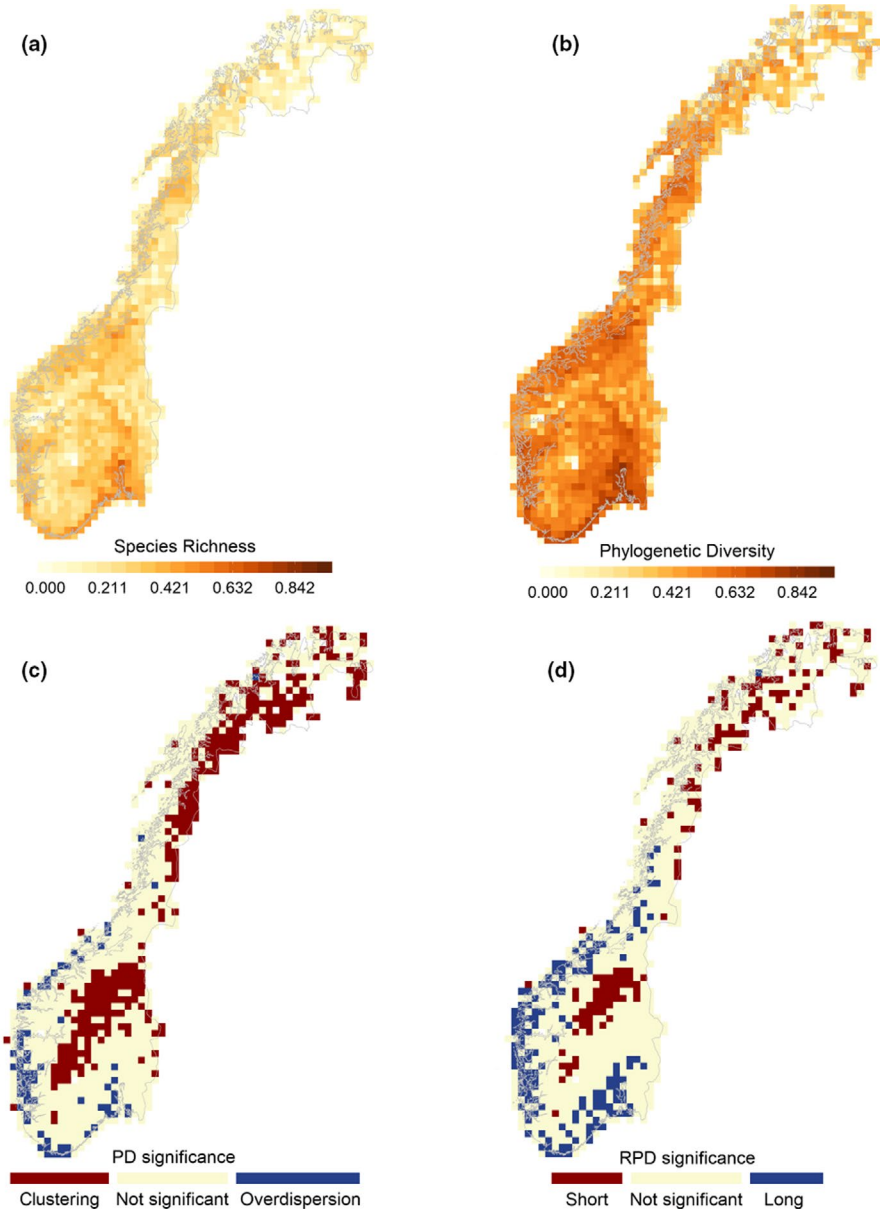

FIGURE 1 (a) Observed species richness. (b) Observed phylogenetic diversity. (c) PD significance; phylogenetic overdispersion (blue) defined as regions with significantly greater PD than expected, and phylogenetic clustering (red) defined as regions with significantly lower PD than expected. (d) RPD significance; areas with significant concentrations of longer branches or shorter branches than expected are shown in blue and red, respectively

1). The highest SR and PD values were found in the south-eastern region of Norway. For both indices, less diversity was observed in mountainous areas and northern Norway. Both SR and PD had high values in areas with greater number of occurrences (Figure A5 in Supplementary information 1).

There was a clear geographical distinction between areas showing phylogenetic overdispersion and phylogenetic clustering. Phylogenetic overdispersion was observed on the coastal areas of southern Norway and phylogenetic clustering in the mountainous areas (Figure 1c). A similar geographical pattern was seen for phylogenetic branch length distributions (RPD) with significant concentrations of long branches along the coast and short branches in the mountains (Figure 1d).

The relative importance and effect of the environmental variables on the four diversity patterns varied (Figure 2). For all patterns, topographic heterogeneity and summer temperature had very high relative importance (Figure 2a). These variables had positive effects on SR, PD and phylogenetic overdispersion, and a negative effect on phylogenetic clustering (Figure 2b,c). Time since last glaciation had also very high relative importance for all diversity patterns (Figure 2a), but the effect on SR was negative and insignificant for PD (Figure 2b). Annual precipitation was important for all variables except PD and had a negative effect on SR and phylogenetic clustering and a positive effect on phylogenetic overdispersion. Soil pH had low importance and was insignificant for all variables except SR where it had a positive effect. Precipitation seasonality was not a significant predictor of any of the diversity patterns (Figure 2).

3.3 | Endemism patterns and potential drivers

The results from CANAPE (Figure 3a) showed concentrations of neo-endemism in the northernmost parts of Norway and more sparsely further south in the mountainous areas. These patterns were very

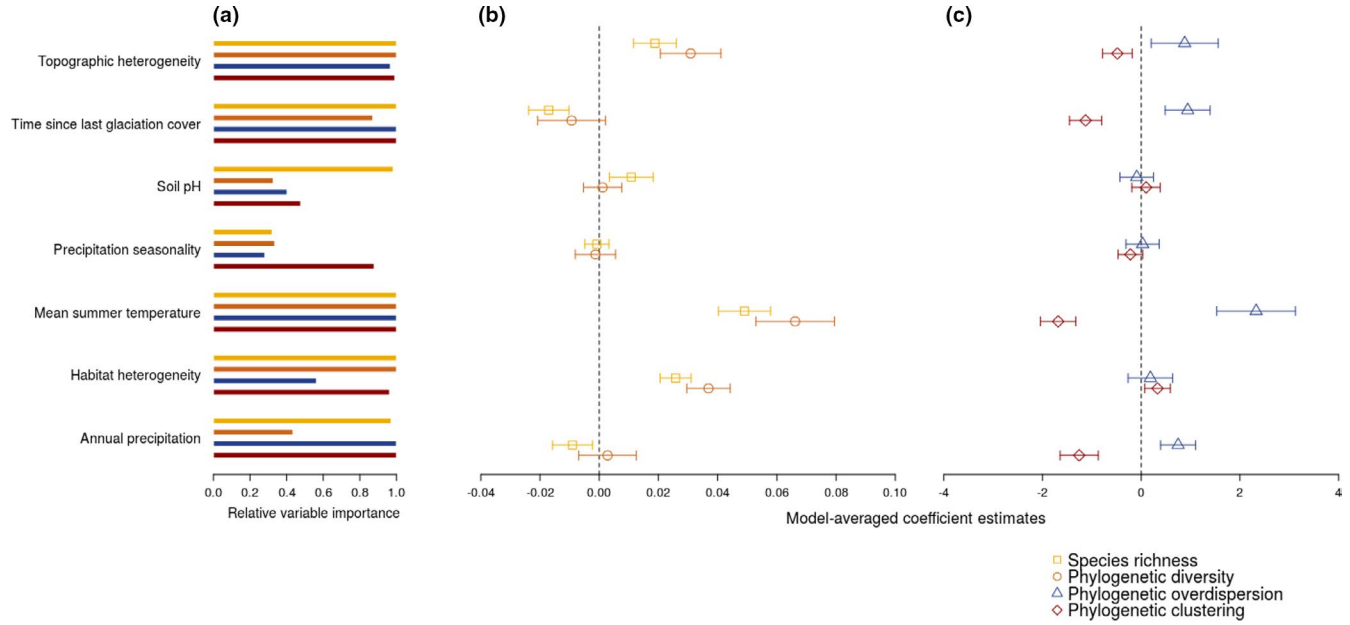

FIGURE 2 Relative variable importance (a) and model-averaged coefficient estimates for SR and PD (b) and phylogenetic clustering and overdispersion (c). The model-averaged coefficient estimates were divided into (b) and (c) because of their difference in parameter estimates due to different model families

different from the observed patterns of WE and PE (Figure A4 in Supplementary information 1), which again were similar to each other. Grid cells significantly dominated by paleo-endemism were not as common: a few cells were identified, mainly on the south-west coast with a few other cells scattered across the region. Centres of mixed-endemism were mainly found along the coast of southern Norway but also scattered across northern Norway. These patterns revealed low annual precipitation (below ~700 mm) and low temperatures (below 11°C) as potential drivers of neo-endemism (Figure 3b).

3.4 | Turnover patterns

RWT and PhyloRWT analyses revealed multiple geographically distinct clusters (Figure 4). Both analyses identified six major clusters (Figure 4a–d), which were compared to Norway's vegetation zones (Figure 4e, Moen, 1999). The alpine and boreal clusters contained more than 70% of the grid cells in both analyses (Figure 4a–d). The major clusters were further divided into minor clusters, some identified as similar to Norway's currently accepted vegetation zones, and these were categorized as boreonemoral and northern boreal (Figure 4). The RWT analysis had a northern alpine cluster that was not apparent in the PhyloRWT analysis (Figure 4a,b).

4 | DISCUSSION

We present the first PD analysis of the whole flora of a post-glacial European region. We found that PD increases towards warmer regions with a higher habitat heterogeneity, and that the highest PD is in the south east of Norway. Phylogenetic overdispersion of plant assemblages appears to be greatest in the milder and wetter regions of Norway, which also have a longer post-glacial history, giving the plants more land-exposed time to disperse into the area. Northern regions, on the other hand, are prone to phylogenetic clustering. Our results indicate that contemporary environmental conditions are strong drivers of PD of the flora of a post-glacial region.

4.1 | Spatial patterns and drivers of diversity

As expected, the observed pattern of PD was similar to that of SR, and areas of higher diversity coincided with higher numbers of occurrence records (Figure A2 in Supplementary information 1). A recent study showed that both observation- and specimen-based occurrences are biased towards areas in Norway with higher human population densities (Speed et al., 2018). The same study also found overrepresentation of occurrences in the warmer regions of Norway, which could potentially lead to incorrect interpretations of a species' ecology and distribution. Nevertheless, the cause and effect relationship between SR and sampling is not straightforward, as collectors are drawn to richer areas, as well as rare taxa, as discussed in Baldwin et al. (2017). Furthermore, despite possible effects of sampling on observed patterns of SR and PD, randomization tests seem robust to sampling biases (Scherson et al., 2017).

Correlation between PD and SR basically serves as the null hypothesis in the randomization applied here: if species co-occur randomly, then one would expect a nearly perfect correlation between PD and SR. The randomization test is designed to find interesting exceptions. For example, we detected many examples of phylogenetic overdispersion and clustering (Figure 1c). These are cases

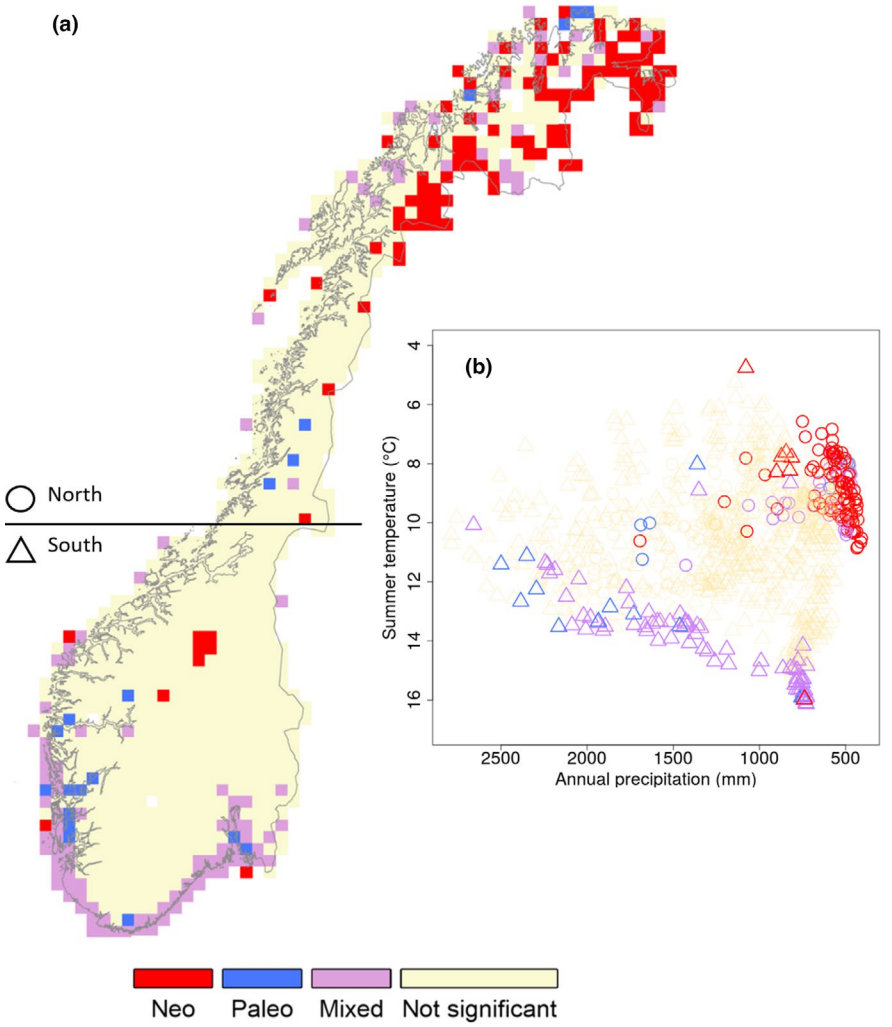

FIGURE 3 Results of CANAPE showing patterns of phylogenetic endemism in Norwegian vascular plants. (a) Red cells show significant concentrations of neo-endemism, and blue cells show significant concentrations of paleo-endemism. Purple cells show areas with a concentration of both. Beige cells are not significant. The black line indicates the midpoint between the northernmost and southernmost extremes of Norway. (b) The distribution of different types of endemism along axes of precipitation and temperature. Southern (cf. a) cells are shown by triangular points, and northern cells by circular points. The axes are ordered as a Whittaker biome plot

where the relationships of species appear to influence their co-occurrence. Phylogenetic overdispersion can be explained with ecological arguments, if closely related species have niche similarities that lead to competitive exclusion (Violle, Nemergut, Pu, & Jiang, 2011). Phylogenetic overdispersion is often found in abiotically low-stress environments (Butterfield et al., 2013). These ecological arguments suggest that cells found in the coastal part of southern Norway contain favourable environments for plants. However, grid cells with both phylogenetic overdispersion and unusually long branches (i.e. significantly high RPD) may indicate that it is the long branches contributing to the pattern of phylogenetic overdispersion rather than distant evolutionary relatedness. As almost all cells with phylogenetic overdispersion also have significantly long branches, it is not possible to exclude that branch lengths drive this pattern. Significant concentrations of long branches alone might indicate the presence of biogeographical refugia, if those clades have been there for a long time, or more likely in the case of southern Norway, indicate the presence of distinct clades that recently immigrated from outside the study area.

Phylogenetic clustering may indicate that the co-occurring species are close relatives that share adaptions for specific conditions (i.e. presence of niche conservatism; Webb, Ackerly, McPeek, & Donoghue, 2002). Co-occurring species could be closely related if there is less competition in more physically stressful habitats (Bruun et al., 2006; Callaway et al., 2002) and that habitat filtering for traits enables these plants to tolerate the stress of Norway's harsh environments (Cavender-Bares, Kozak, Fine, & Kembel, 2009). This could explain why Norway has more cells with phylogenetic clustering than with phylogenetic overdispersion. Grid cells containing unusually short branches (i.e. significantly low RPD) might indicate centres of recent diversification. On the other hand, grid cells with phylogenetic clustering, but lacking unusually short branches, may indicate that the pattern is driven more by clustering of relatives than by recent diversification. Grid cells like these are found scattered across Norway, suggesting that it is close evolutionary relatedness that is indeed creating this pattern. Thus, it is useful to contrast PD significance and RPD significance patterns.

All of the environmental variables tested were, in general, important in explaining the diversity patterns (Figure 2). Summer temperature was important for all diversity patterns and had the largest relative effect, which is unsurprising and concordant with our prediction (*P2*), as temperature was found to drive plant diversity (Allen et al., 2002).

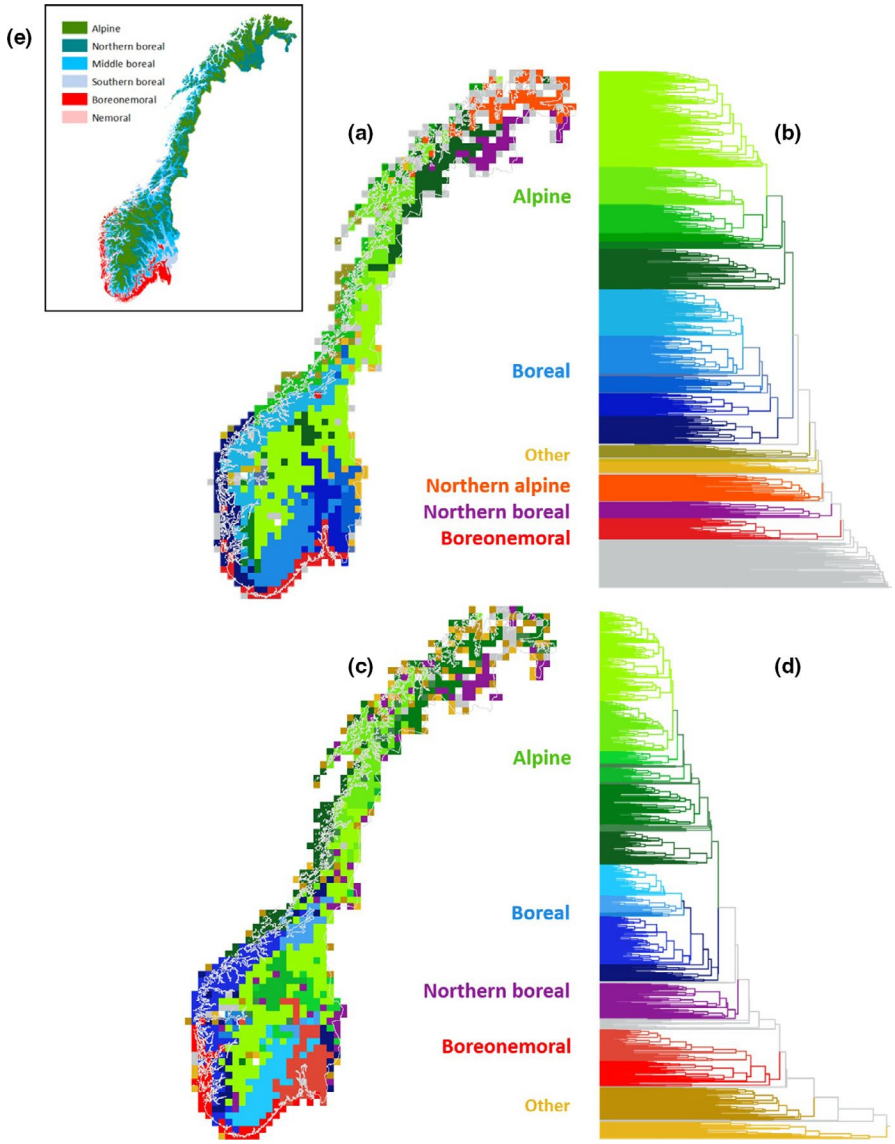

FIGURE 4 Range-weighted species turnover (a, b) and range-weighted phyloturnover (c, d) analyses. The analysis compares all grid cells, and clusters the cells together using UPGMA, by looking at the species or branches they share, but giving less weight to wide-ranged species or lineages (Laffan et al., 2016). (a, c) Map of Norway that indicates the geographical position of the cell clusters in the turnover topology (b, d). Clusters are coloured by their similarity to Norway's vegetation zones. Clusters named 'Other' had no clear geographical clustering. (e) Map of vegetation zones in Norway, which was used to categorize the grid cells clusters (adapted from Moen, 1999. See Figure A6 in Supplementary information 1 for higher resolution)

A limitation for vascular plants in Norway is not necessarily that the temperature becomes too high, which may be an issue in areas with low water availability, but rather the opposite. Phylogenetic clustering of taxa was found in areas with lower temperatures, as expected (*P1*), which suggests the particular clades present in those areas are cold-tolerant (Donoghue, 2008). While it is important to remember the potential sampling bias towards warmer regions (Speed et al., 2018), the suggested effect of temperature on the SR and PD patterns was relatively high. Topographic heterogeneity is also inferred as a very important driver, with expected (*P2*) positive correlations with SR, PD and phylogenetic overdispersion, and negative effects on phylogenetic clustering. Variation in elevation provides ecological space for diverse species with different specializations, and thus higher PD. Similarly, habitat heterogeneity has the expected positive correlation with SR and PD. However, this variable was not significant for either phylogenetic overdispersion or clustering. Time since last glaciation cover was positively correlated with phylogenetic overdispersion and negatively correlated with phylogenetic clustering, supporting our prediction (*P3*) and could suggest that greater competition develops over time as community associations age, or stronger environmental limitation in younger regions. This parallels a previously reported pattern of higher intra-specific plant genetic diversity in regions of Scandinavia that have been ice-free for a longer time (Westergaard et al., 2019).

4.2 | Spatial patterns and potential drivers of endemism

The observed pattern of PE showed elevated levels along the coast of southern Norway, but additional patterns were found via the CANAPE approach. Cells dominated by paleo-endemism were located mainly on the coast of southern Norway. We found that almost all paleo-endemic cells were located in areas with an annual precipitation ~1,400 to 2,600 mm and summer temperatures ~11 to 14°C. This was also seen in a previous study on ferns where paleo-endemics are mainly found in well-watered environments with non-extreme temperatures (Jordan, Harrison, Worth, Williamson, & Kirkpatrick, 2016).

Previous discussions about potential *nunataks* propose the existence of such areas in the southwestern part of Norway (Brook, Nesje, Lehman, Raisbeck, & Yiou, 1996) and on mountaintops on the coast of northern Norway (Alm, 1993; Parducci et al., 2012; Vorren, Vorren, Alm, Gulliksen, & Løvlie, 1988). Earlier studies using spatial phylogenetics have suggested that a concentration of range-restricted, long branches may reflect a refugium where lineages with few living close relatives have been isolated for a long time (Mishler et al., 2014; Scherson et al., 2017). Still, areas seen as dominated by paleo-endemism do not necessarily imply that the lineages present in that area also originated there (Grandcolas, Nattier, & Trewick, 2014). Rather, this means that the identified cell contains long phylogenetic branches that are spatially restricted. Although our methods did not identify any cells dominated by paleo-endemism in areas previously hypothesized to contain *nunataks*, some areas of mixed endemism in southwestern Norway do overlap with hypothesized *nunataks*. Still, we conclude that climatic drivers are more probable in explaining our observed patterns of paleo-endemism in Norway.

Note that the relative endemism measures applied here are only relevant to the study area. Therefore, we are measuring only regional endemism; many of the long-branch lineages in southern Norway are more widespread beyond the southern limit of our study area. The difference between local and global endemism was discussed by Thornhill et al. (2016, 2017), who noted that while global spatial phylogenetic studies will be welcome once they are possible (overcoming data gaps that are prohibitive at present), local endemism is of scientific interest and a relevant concern for conservation within a management region.

Cells dominated by neo-endemism were mainly located in the northernmost areas of Norway. Recently evolved polyploid species, which increase with latitude and altitude (Grytnes, 2003; Mable, 2004), are a possible cause of this pattern. For these neo-endemic cells, annual precipitation and summer temperature appear to be clear drivers. The combination of low temperatures and low precipitation can produce stressful conditions for plants, which may lead to sparsely filled habitats and ecological opportunities. Very few studies have investigated how stress leads to speciation in plants (Bijlsma & Loeschcke, 2005; Lexer & Fay, 2005), but it has been suggested to be an important factor and could explain our observed pattern of neo-endemism. Notably, the Dovre mountain range of southcentral Norway also contained a distinct and spatially disjunct cluster of neo-endemism (Figure 3b). This mountain range comprises unique, regionally important occurrences of species, populations and vegetation types (Elven, Fremstad, Hegre, Nilsen, & Solstad, 1996). The area has for many years been discussed as a possible ice-free glacial refugium because of its richness in alpine plant species and their disjunct distributions in northern Fennoscandia (e.g. the controversial 'overwintering theory' of Nordal, 1987; Sernander, 1896, 1908). A biostratigraphic study of two lakes located in Dovre concluded that the region contained ice-free areas as early as 17–18 kyr cal BP (Paus, Velle, & Berge, 2011). If so, glacial refugia may explain our observations of elevated richness of alpine vascular plants in Norway's central mountains.

Almost all northern mixed endemism cells were found in regions with mean summer temperatures below 11°C, while the southern mixed endemism cells were found above 12.5°C. These cells are concordant with suggested post-glacial immigration routes (Moen, 1999). The northern mixed endemism cells may reflect lineages that immigrated from the east, which are limited by mild winters. Since the temperature variable in this study was highly correlated with other temperature variables in Norway (Speed & Austrheim, 2017), among them winter temperature, we argue that there would be a positive correlation between cold winter temperatures and northern mixed endemism cells. The southern mixed endemism cells contained lineages limited by both cold summers and winters, and the inhabiting plants may have immigrated from the west and south.

4.3 | Species and phylogenetic turnover patterns

The RWT analysis (Figure 4a,b) and the PhyloRWT analysis (Figure 4c,d) resulted in distinct clusters of the vascular plants in Norway based on species and on phylogenetic branch lengths, respectively. In the PhyloRWT, almost all of the clusters showed a non-random geographical signal in their distribution, which suggests that there is an evolutionary signal in the distribution of the vascular flora of Norway. Comparison of RWT and PhyloRWT revealed both to have two very distinct clusters with distributions resembling the alpine and boreal vegetation zones in Norway. For the alpine subclusters, both analyses revealed a boundary in mid-northern Norway. Underpinning the biological importance of this area, this boundary coincides with results from Berglund and Westerbergh (2001) on the plant *Cerastium alpinum* in Norway, and is reminiscent of a previously reported 'suture-zone' that spans mid-Norway and mid-Sweden and is associated with mammalian post-glacial colonization (Taberlet, Fumagalli, Wust-Saucy, & Cosson, 1998). The boreonemoral cluster was observed on the coast of southern Norway in both turnover analyses, coinciding with a large number of species, the highest levels of observed PD and the areas of mixed endemism.

In general, the plant communities defined by PhyloRWT resemble previous maps of Norway's vegetation more closely than those of RWT. The better regionalization of plants in PhyloRWT reflects its inclusion of relationships among species and branch lengths in the turnover measure (Laffan et al., 2016). The patterns seen may thus be partly explained by historical biogeography but are also likely caused by phenotypic sorting where communities differ from each other in lineages with differing environmental preferences (Webb et al., 2002). This may cause closely related species to co-occur due to their conservation of those traits important for the different environments (Cavender-Bares, Keen, & Miles, 2006). This is however not seen in the RWT analysis, which is based only on species and does not fully take into account evolutionary and ecological similarities.

4.4 | Conclusions and future implications

In this study, we show that despite its relatively recent origin via post-glacial colonization, Norway's vascular flora is non-randomly distributed in space in terms of evolutionary history. Geographical

patterns in phylogenetic composition are distinct from those of species composition, highlighting the importance of assessing evolutionary relatedness when determining community assembly. We find that the drivers of species and PD patterns are likely both ecological (spatial heterogeneity and climatic) and historical (direction of colonization and time since last glaciation cover), so future environmental change is likely to influence PD patterns.

Today, the climate is changing rapidly, with temperatures increasing especially in Europe and the Arctic (Smith, Edmonds, Hartin, Mundra, & Calvin, 2015). As summer temperature appeared to have a strong, positive effect on SR, PD and phylogenetic overdispersion, and a negative effect on phylogenetic clustering, we can predict that an increase in temperature through global warming may lead to a shift in phylogenetic composition of communities. Ecosystems with phylogenetically clustered species may become less robust (Tan, Pu, Ryberg, & Jiang, 2012). As phylogenetically clustered species are mainly found within the northern and alpine regions of Norway, these are likely under greater threat due to climatic change. Current centres of endemism might shift or disappear (González-Orozco et al., 2016). Thus, it will be important to monitor patterns of PD into the future.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.0p2ngf1vx, https://doi.org/10.5061/dryad.j9kd51c7j, https://doi.org/10.5061/dryad.kkwh70s1n).

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BIOSKETCH

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Author contributions: M.D.M., J.D.M.S. and B.D.M. conceived the study. I.M.M. and M.D.M. performed the sampling and laboratory work. I.M.M., J.D.M.S., A.H.T., M.D.M. and M.B. performed the analyses and interpreted the results. I.M.M. led the writing with input from all co-authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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