ORIGINAL RESEARCH

Spatial patterns of phylogenetic and species diversity of Fennoscandian vascular plants in protected areas

Damaris M. Matten[1] · Ida M. Mienna[1,2,3] · Vanessa C. Bieker[1] ·
Brent D. Mishler[4] · Victoria S. Moen[1,5] · Malene Nygaard[1,6] ·
Katariina E. M. Vuorinen[1,7] · Mika Bendiksby[1,2] · Michael D. Martin[1] ·
James D.M. Speed[1]

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Abstract

Protected areas are one of the main strategic means for conserving biodiversity. Yet, the design of protected areas usually neglects phylogenetic diversity, an important diversity measure. In this paper we assess the phylogenetic diversity and species richness of vascular plants in Fennoscandian protected areas. We evaluate how much species richness and phylogenetic diversity is found within and outside protected areas, and the differences in plant diversity between different categories of protected areas. We also assess the differences in the diversity-area relationship of the different protected area categories in terms of both species richness and phylogenetic diversity. We build a multi-locus phylogeny of 1,519 native vascular plants of Norway, Sweden, and Finland. We estimate the phylogenetic diversity and species richness by combining the phylogeny with publicly available occurrence data and the currently protected area system of Fennoscandia. Our results indicate that protected areas in Fennoscandia hold more plant diversity when larger, and that phylogenetic diversity increases faster with area than species richness. We found evidence for more plant diversity outside of protected areas of the different countries of Fennoscandia than inside of protected areas, but no evidence for plant diversity differences between areas with different protection status. Hence, our results indicate that the current protected area system in Fennoscandia is no more effective in conserving phylogenetic diversity and species richness of vascular plants than a random selection of localities. Our results also indicate that planning conservation strategies around phylogenetic diversity, rather than species richness, might be a first step to protect vascular plant diversity more effectively.

Keywords Biodiversity · Spatial phylogenetics · Conservation · Diversity-area relationship · Flora

Extended author information available on the last page of the article

Introduction

A major motivation in establishing protected areas is to conserve biodiversity. Protecting biodiversity ensures current and future ecosystem services, and the livelihood of cultures and local communities (e.g., McNeely 1994; Pisani et al. 2021). Location and size of the priority area are some key components for successful protection of biodiversity (Donaldson et al. 2021). One method of conserving biodiversity is the protection of hotspots — places that hold exceptionally high concentrations of species and rare, threatened or endemic species (Myers et al. 2000; Reid 1998) — as this slows biodiversity loss in the protected region by conserving many species in a single region (Kobayashi et al. 2019).

The prioritised location and size of an area for protection will depend on the way biodiversity is measured and quantified (Brum et al. 2017). One definition of an effective biodiversity measurement is that it serves to reach a goal, where the goal can be economic, ecological, social, or political (Joppa et al. 2008). Since there is a large variety of biodiversity measures (e.g., genetic, species, and ecosystem diversity), the measure's suitability will depend on the goal. One measure will for example be better suited for defining regions to protect species from extinction, whilst another measure will better identify areas for protecting the range of habitats in a region (Davies and Cadotte 2011; Yadav and Mishra 2013). Oftentimes however, diversity is not considered when planning for protected areas, because economic decisions outweigh diversity (Venter et al. 2018).

Traditionally, biodiversity within an area has been quantified for conservation actions using species richness (SR) as the sole measure, mostly because it is easy to calculate (Karanth et al. 2019). However, SR only captures one dimension of biodiversity. As such, protected areas are usually established based on the premise that SR equates to biodiversity (Capmourteres and Anand 2016; Margules and Usher 1981). However, using SR as the sole measure of biodiversity ignores the evolutionary and functional dimensions of diversity. Consequently, we might fail to protect areas that are highly valuable for their inherent ecosystem services just because they are lower in the single measure "SR" by other areas (Kareiva and Marvier 2003).

An area's evolutionary diversity is assumed to correspond to the community's resilience and capacity to respond adaptively within the species to disturbance, maintaining a resilient ecosystem (Faith 2018). An increasingly used measure of biodiversity reflecting evolutionary diversity is phylogenetic diversity (PD), which quantifies the evolutionary distance among taxa (Cadotte et al. 2009; Mishler et al. 2014). Using PD in conservation strategies promises to protect the total evolutionary history, which has been shown to connect to the evolutionary potential of a species in a certain region, adding valuable information and improving conservation (Cadotte et al. 2012; Quan et al. 2018; Winter et al. 2013). Moreover, as closely related species tend to have similar traits, PD is generally also a measure of functional diversity (Cadotte et al. 2008). In postglacial landscapes both evolutionary processes and colonization histories combined determine diversity patterns (Mienna et al. 2020).

If conservation priority decisions are made based on a single or inappropriate measure of biodiversity, one is at risk of inducing a spatial mismatch of protected areas and areas of biodiversity, for which there are several examples for terrestrial mammals (Brum et al. 2017). Even though SR and PD are often highly correlated (Aguilar-Tomasini et al. 2021; Mienna et al. 2020), divergent patterns can be hidden (Forest et al. 2007). This can be the

case when high SR is represented by a large number of closely related species (Knapp et al. 2008; Mishler et al. 2014; Scherson et al. 2017), or when a low SR is represented by species that are distantly related (i.e., with long branch distances between the species in the community; Mishler et al. 2014; Scherson et al. 2017). It is therefore important to combine various measurements of biodiversity in order to reveal hidden patterns and reduce spatial mismatch between protected areas and high biodiversity regions (Carta et al., 2019). Revealing such hidden patterns can improve targeted conservation actions and add valuable information about species assemblages (Knapp et al. 2008; Magurran 2021).

Unfortunately, protected areas often do not correspond to areas with the highest biodiversity (e.g., Brum et al. 2017; Daru et al. 2019; Rodrigues et al. 2004). This is mainly due to the considerable interest in high biodiversity areas from an economic standpoint (e.g., for agriculture). Hence, many high biodiversity regions have been exploited or are threatened by land-use change (Cincotta et al. 2000; Gaston et al. 2008; Kong et al. 2021). Because of the high value for human exploitation, prioritisation decisions induce a bias in the placement of protected areas towards areas less valuable to humans (Joppa and Pfaff 2009). Protected areas are often established in places which are unproductive for human purposes and are naturally less diverse, like high in mountainous areas and in northern regions. The productive areas are used for agricultural purposes, and urban areas have developed in these areas. Protecting biodiversity effectively is also dependent on the size of the protected area. Biodiversity generally increases with area size (Rosenzweig 1995), making the use of diversity-area relationships relevant in planning for conservation purposes (Desmet and Cowling 2004). A large area can provide a wide variety of habitat types and environmental conditions, thus increasing the range of niches. A very large area does not have an infinite number of species, however. At some point, possible habitat types and environmental conditions are saturated and the number of included species levels out. The relationship between SR and area size (SAR) is well studied. PD area relationships (PDAR) have not received as much attention. It has been shown, however, that maximum values of biodiversity in biodiversity hotspots are faster reached in PDAR than in SAR (Mazel et al. 2014, 2015; Morlon et al. 2011). This could also apply to areas outside of biodiversity hotspots and for a variety of taxa. Looking at diversity-area relationships rather than only SAR can help better conservation strategies and further understanding of ecology and biogeography, focusing on communities, rather than populations and allowing to explore habitats and survival of species (Mazel et al. 2015; Rosenzweig 1995). Diversity-area relationships also help to understand the responses to the environment of species (Li et al. 2018), and can predict the loss of evolutionary history through loss of habitat (Morlon et al. 2011).

Protected areas in higher latitude countries may become more important in the future, because they may serve as refugia for species under pressure from climate changes (Berteaux et al. 2018). The diversity in these areas is already shaped by postglacial processes. Areas rich in species are generally found at lower elevations and latitudes, such that high latitude countries hold less species than lower latitude countries (Kreft and Jetz 2007; Rahbek 1995; Rahbek et al. 2019). Under a warming climate, species' ranges are expected to shift poleward and to higher elevations, which has been observed for a variety of species in water and on land (e.g. Plantae, Vertebrata, Invertebrates; fish stocks; Tracheophyta; Invertebrates; Maclean and Wilson 2011; Palacios-Abrantes et al. 2022; Pauli et al. 2012; Platts et al. 2019).

In this study, we investigated how well the native Fennoscandian vascular plant diversity is represented within protected areas, focusing on the protected areas that are IUCN categorised. We compared phylogenetic diversity and species richness, and we assessed whether the different IUCN categories of protected areas conserve plant diversity to different extents. We hypothesised that (H1) phylogenetic diversity and species richness of vascular plants will generally be higher outside of protected areas than inside; that (H2) protected areas with a stricter protection status (category Ia, Ib, II and III) have a higher species and phylogenetic diversity than those with a less strict protection status (category V and VI); and lastly, that (H3) phylogenetic diversity shows a stronger increase with area than does species richness.

Materials and methods

Species list

The list of native vascular plant species in Norway was obtained from Mienna et al. 2020), which was originally based on data from the Norwegian Biodiversity Information Centre (NBIC) and modified to the recent version of the national flora (Lid and Lid 2005). Species were excluded from the list of natives when they were listed as: "introduced on purpose after 1800", "introduced on purpose but not naturalised before 1800", "introduction history uncertain or unknown", or "not found". The species lists from Sweden and Finland were obtained from their corresponding national institutions (i.e., *SLU Swedish Species Information Center | SLU Artdatabanken*, 2017, downloaded 17.01.2017 and *Finnish Biodiversity Information Facility*, 2017, downloaded January 17th 2017) and modified in the same manner as for the Norwegian flora (Mienna et al. 2020). Additionally, when a species was divided into subspecies on the species list for Sweden, we included the species only if at least one subspecies was marked as native for Sweden. As the status of the species was not marked in the Finnish vascular plants list, we consolidated the "Field flora of Finland" (Hämet-Ahti et al. 1998). Species were removed if they were not listed in the "Field flora of Finland" and if the species had alien status in Finland, Sweden, and Norway (DASIE). Species not found in either "Alien species of Europe" or the "Field flora of Finland " were checked in the Euphrasia checklist of Nordic vascular plants (*euphrasia.nu – Nordens kärlväxter*, 2017) and retained if marked "in Scandinavia before 1700". The list of native vascular plant species in Fennoscandia included 1620 species.

Occurrence data and protected areas

We downloaded species occurrence data for all vascular plants in Fennoscandia from the Global Biodiversity Information Facility (Gbif.Org, 2020; accessed 24.07.2020) and filtered the data by the above-mentioned species list. We included both occurrences based on observations and preserved specimens. As both types of occurrence records are complementary in terms of different taxa, space ,and time (see e.g., Speed et al. 2018), using both increases the number of records and their coverage. From the occurrence data we extracted the species specific GBIF identification numbers, the species key (and where the species key was not available, instead we extracted the usage key), and searched for synonyms with the R packages "rgbif" and "Taxonstand" (Cayuela et al. 2021; Chamberlain and Boettiger 2017)

and checked manually for ambiguous results with the "World Flora Online" (WFO 2022). Species with less than three occurrences in Fennoscandia were excluded, as were occurrences older than the year 1900. Occurrences with spatial issues were removed, including those with coordinate uncertainties of >2 km, and occurrences outside of the borders of Fennoscandia.

Protected areas have varying management and governance types between countries. The IUCN has established a global framework in its protected area management categories, organising the spectrum of protected areas into six categories (Dudley 2008; Table 1).

The use of these categories allows comparison between areas and countries, which would otherwise be difficult (UNEP-WCMC and IUCN 2020). The six categories range from strictly protected areas (Ia – II) to areas that are less strictly protected (III-VI). These area categories differ in both size and objectives; some aimed at protecting specific species or landscapes, whereas others aim at conserving biodiversity in general.

We obtained polygons for the protected areas from the World database of protected areas (WDPA; UNEP-WCMC and IUCN 2020), and used all IUCN-classified (IUCN categories Ia, Ib, II, III, IV and V) terrestrial protected areas (PA) in Finland, Sweden and Norway (Table 1). We did not use protected areas represented as points in the WDPA database, and we removed areas which did not have an IUCN category assigned (i.e., status "not assigned", "not applicable" or "not reported").

We rasterized the protected area polygons to a 15×15-km grid with 11,656 grid cells (WGS 84/UTM zone 32 N). To avoid a double count of occurrences when protected areas were overlapping, we retained the more strictly protected area when rasterizing. The protected area grid was used for comparison between protected and unprotected areas. Protected areas with less than three species and less than three occurrence records were removed. Because sizes of protected areas vary and precision gets lost when analysing biodiversity in a raster grid, further diversity analysis was conducted on the polygons of the protected areas rather than the raster grid.

DNA extraction and sequencing

We generated 264 new nuclear ribosomal internal transcribed spacer (ITS) sequences from specimens deposited in the herbaria O (Natural History Museum, Oslo) and TRH (NTNU University Museum, Trondheim; Table S2). DNA extraction, amplification of the *ITS* region, and Sanger sequencing of the resulting PCR product followed the procedures described by Mienna et al. (2020), with two notable exceptions. Firstly, for all specimens collected before the year 2000, DNA was extracted and prepared for PCR amplification in the NTNU University Museum's dedicated, UV-sterilised, positively pressurised paleogenomics laboratory facility. Secondly, herbarium specimens yielding degraded DNA extracts, from which we could not amplify the entire *ITS* region using the primer pair ITS5a/ITS4 (Stanford et

Table 1 List of IUCN categories used for grouping protected areas in this Fennoscandian study

IUCN category	Type of area
Ia	Strict Nature reserve
Ib	Wilderness area
II	National park
III	Natural monument
IV	Habitat/Species management
V	Protected Landscape

al. 2000; White et al. 1990), were subjected to additional attempts amplifying the region in two shorter fragments, targeting *ITS1* and *ITS2*, respectively, using the primer pairs ITS-p2/ITS-p5 and ITS-p3/ITS-p4 (Cheng et al. 2016). The PCR of these two *ITS* fragments were conducted in 50-µl reaction volumes containing the following components: 5.0 µL template DNA extract, 1.25 units AmpliTaq Gold™ DNA Polymerase, 0.4 mg/mL bovine serum albumin (BSA), 0.2 µM each primer, 1.5 mM MgCl2, 0.25 mM each dNTP, and 1x AmpliTaq PCR Buffer II. The PCR protocol was as follows: 4 min of initial denaturation at 94 °C; 40–45 cycles of 30 s at 94 °C, 40 s at 55 °C, 60 s at 72 °C, followed by 10 m final extension at 72 °C. PCR products were electrophoresed, and those with a single, appropriately sized band of DNA were chosen for Sanger sequencing at the commercial provider Eurofins Genomics (Germany). We used the same primers for sequencing as we did for the PCR amplification.

Sequence alignment and phylogenetic analysis

We obtained the *ITS*, maturase K (*matK*) and ribulose-1,5-bisphosphate carboxylase- oxygenase (*rbcL*) sequences of Norwegian vascular plants from Mienna et al. (2020) and used Matrix Maker (Freyman & Thornhill, Andrew H., 2016/2020) to supplement this dataset with sequence data for additional species from GenBank (Benson et al. 2018) and Boldsystems (Ratnasingham & Hebert, 2007), as well as from our own newly generated sequences. We used Mafft Version 7.450 (Katoh and Standley 2013) to perform an automated alignment of the existing sequences and the 264 newly generated sequences (Table S2). The existing Norwegian three-marker alignment (*ITS*, *matK* and *rbcL*, Mienna et al. 2020) was concatenated with the newly generated sequences (*ITS*) and sequences from the public databases of the Swedish and Finish taxa into a multiple sequence alignment.

Several maximum-likelihood phylogenies were generated using RaxML-HPC v.8 (Stamatakis 2014) under the GTRGAMMA nucleotide substitution model and using a partition for each of the three loci on the CIPRES Science Gateway (Miller et al. 2010). 1000 bootstrap support replicates were run in each phylogenetic analysis. As in Mienna et al. (2020), we rooted the tree using Pteridophyta. The resulting tree was verified by comparing it to the plant family phylogeny by the Angiosperm Phylogeny Group IV (APG IV, Chase et al. 2016; Stevens 2001). In cases where an accession was misplaced according to the APG IV phylogeny or genus assignment or occurred on relatively long branches, the alignment was checked for obvious errors in homology inference. After manual correction and removal of highly ambiguously aligned regions, the process was repeated. Accessions that remained problematic were excluded from downstream analyses.

Diversity patterns

SR and PD were calculated for all raster grid cells. SR was calculated as the sum of the individual species in each grid cell. To make analysis more robust by only including well sampled cells, those cells with fewer than 50 occurrences and fewer than 20 species were excluded from further analysis. PD was calculated as the sum of total branch length spanning the species within each grid cell or protected area polygon using R package "picante" (Kembel et al. 2010). Using the R package "canaper" (Nitta et al. 2022; Nitta and Iwasaki 2021), we performed null-hypothesis randomisation tests of PD to find areas of phyloge-

netic clustering or overdispersion and randomizations of relative PD (RPD) to find concentrations of long or short branches. To compare diversity and account for possible spatial autocorrelation between inside and outside of protected areas, we constructed generalised additive models with a smoother on the midpoint coordinates of each grid cell, using R package "mgcv" (Wood 2011, 2017; Wood et al. 2016). We included net primary productivity of the warmest month and temperature of the warmest quarter to explore the differences between inside and outside of protected areas.

Precision is lost when working with grid cells, therefore the protected area polygons were used in the following analysis to get a better picture of species area relationships in protected areas. Because we work with publicly available occurrence data, which is not equally sampled and covers differently sized areas, we checked if the areas had been sufficiently sampled. We used rarefaction with Hill numbers with R package "iNEXT" (Chao et al. 2014; Hsieh et al., n.d.). This method describes the sample completeness of the whole community, including species that have not yet been sampled (Roswell et al. 2021). We tested the hypothesis that PDAR is steeper than SAR using generalised mixed models with a negative binomial distribution for SR and a tweedie distribution for the PD.

Results

Molecular and spatial data

The final molecular dataset included 1,564 accessions (all different species), of which 264 are represented by newly generated sequences for the present study (Table S2). Of all included species, 389 were represented by the *ITS* locus only, 15 by *matK* only, 38 by *rbcL* only, 842 by all three markers and the remaining species by a combination of two markers. Lengths of the alignments of the respective loci were 3,582 bp for the *ITS*, 2,353 bp for *matK*, and 1,390 bp for *rbcL*. The phylogenetic tree, based on the concatenated, three-loci, 7,325 bp long alignment, was generally well resolved with monophyletic groupings corresponding to the orders and families of the APG IV (Figure S2). A total of 1,519 species were present in both the phylogeny and in the occurrence datasets, which were used for all subsequent analyses. We used the inferred number of mutations as the branch lengths (a "phylogram"; Mishler 2023).

Spatial patterns of species richness and phylogenetic diversity

The final spatial dataset contained 8,574,293 records in 11,656 cells in a 15×15-km grid (WGS 84/UTM zone 32 N). The cell with the highest SR and PD was found in the southeast of Sweden (SR: 923 species, PD: 67.83 branch length units), and was outside of all protected areas. The spatial patterns of SR and PD were similar (Fig. 1, Figure S3, correlation coefficient: 0.96), with higher plant diversity in the south (southern Norway and Sweden) and less towards the north, particularly in the mountainous ranges.

Some small differences between the patterns of PD and SR were visible at the northern coastline of Norway, in the northern Scandinavian mountains and in some southern parts of Fennoscandia, where PD was lower than would be expected from SR (phylogenetic clustering). More PD than expected can be found scattered throughout Fennoscandia, but more
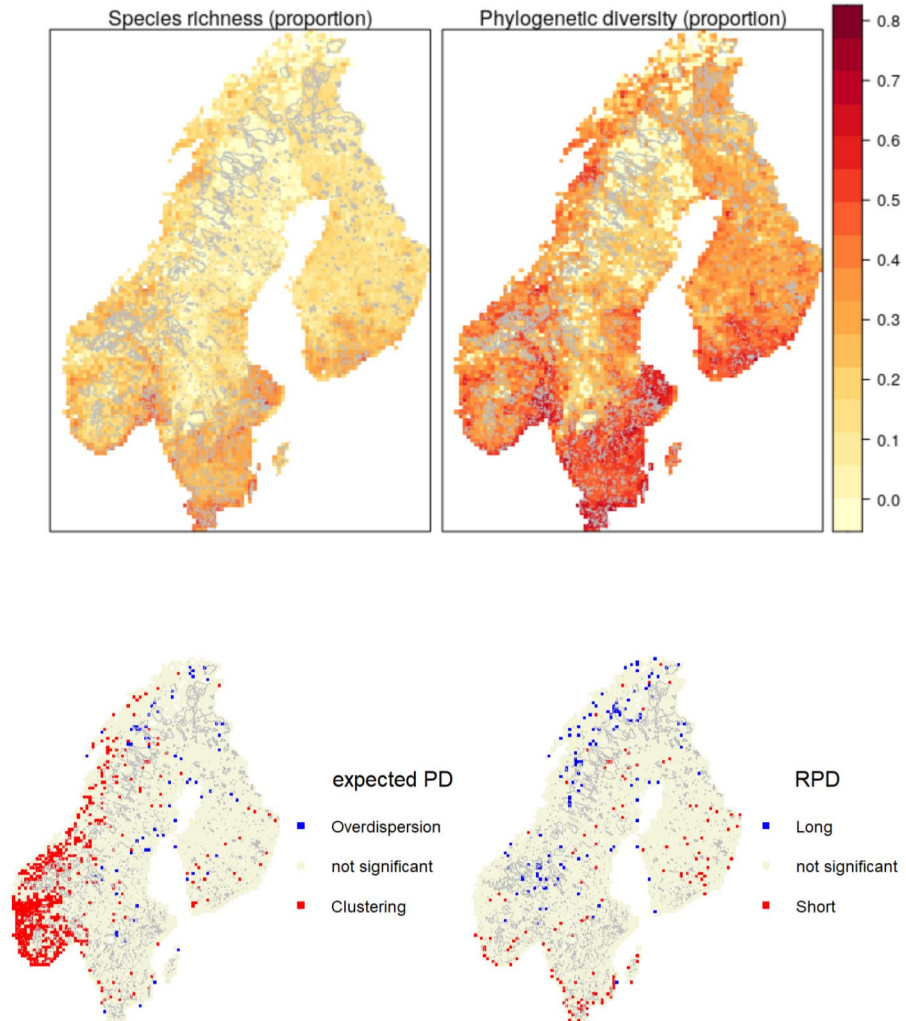
Fig. 1 The top panel shows the proportion of total plant species richness (left) and proportion of total phylogenetic diversity (right) on a 15×15 km grid. Areas with darker colour contain higher diversity proportions, and areas with lighter colour lower proportions. The lower panel on the left shows grid cells with significantly less or more PD than expected (p-value > 0.05), with red representing phylogenetic clustering (less PD than expected) and blue phylogenetic overdispersion (greater PD than expected). The lower panel on the right shows grid cells with significant less or more relative phylogenetic diversity than expected, with blue representing a concentration of long branches and red a concentration of short branches. Protected areas are shown as grey outlined polygons on the maps

towards the north. At the southern coastline, cells with a concentration of shorter branches can be found and in central and north of Fennoscandia a concentration of longer branches can be found).

A total of 4,262 IUCN-categorised protected areas were included with 764 in Finland, 1,069 in Norway and 2,429 in Sweden (Figure S1). The sizes of the areas varied from

0.0004 km² to 5,662.55 km² (Table S1). The comparison of diversity measures inside and outside of protected areas were conducted on the 15×15-km grid and showed that there was a significant difference in SR or PD between protected and unprotected areas of the different countries, with the difference in diversity between inside and outside protected areas between 5 and 15% of estimates (Fig. 2, Figure S4, Table S3).

Protected areas also had a lower net primary productivity (median: 104.23, 117.53; Q1: 92.67; Q4: 152.56) and mean temperature (median: 9.94; Q1: 8.42; Q4: 10.91) compared to unprotected areas (NPP median: 203.84; Q1: 161.93; Q4: 228.95, temp median: 13.20; Q1: 11.23; Q4: 14.72; Figure S4). All 1,519 included species had at least one occurrence outside the protected areas, and 108 of these species were not recorded within any of the included protected areas (Table S4). Of these 108 species, seven are on the Finnish red list for species, 46 are on the Swedish red list, and 26 are on the Norwegian red list (near threatened, vulnerable, critically endangered, and regionally extinct, Table S4). Only one of the species consistently occurring outside protected areas was also threatened in all countries; this species is *Hippuris tetraphylla*, listed as vulnerable in Norway and Finland, and critically endangered in Sweden.

The species accumulation curves (Fig. 3) for all but one protected area category reached an asymptote, indicating generally sufficient sampling. The exception was category III, which also had the lowest number of occurrence records (10,556 records).

Comparing diversity measures within the different categories of protected areas showed that highest SR can be found in categories V and II (408 species and 394 species), and highest PD in categories V, IV and II (42.77 branch length units, 39.54 branch length units and 39.33 branch length unit; Fig. 4, Figure S1).

The highest plant diversity both in SR and PD can be found in categories II and V, when looking at the unscaled numbers, when scaled by area size categories III and IV have higher diversity. The predicted relationship between diversity and area, shows that both the highest overall diversity and the highest diversity in smaller areas was found in category V (max size: 1206.31 km², Table S1). In category Ia and Ib the diversity was lowest, even in larger areas, though their confidence intervals did overlap with all other protected area types
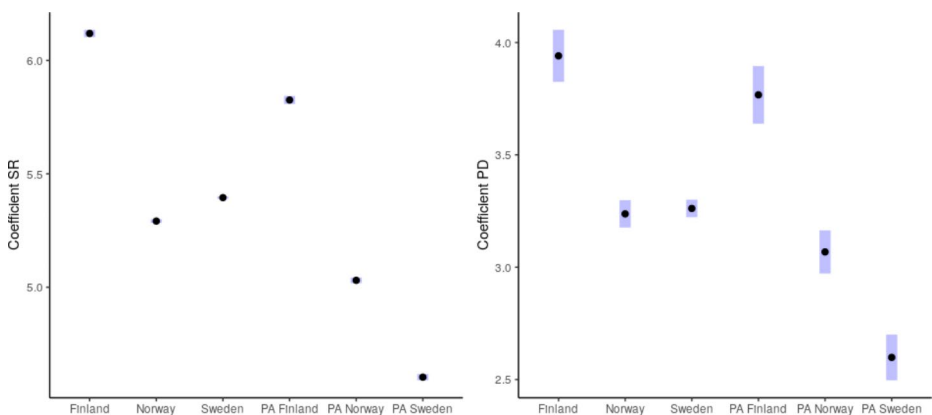

Fig. 2 Coefficients of the generalised additive model comparing plant diversity measures outside of protected areas (Finland, Norway, Sweden) and inside protected areas (PA Finland, PA, Norway, PA Sweden), with species richness on the left and phylogenetic diversity on the right. Standard errors are displayed in light blue
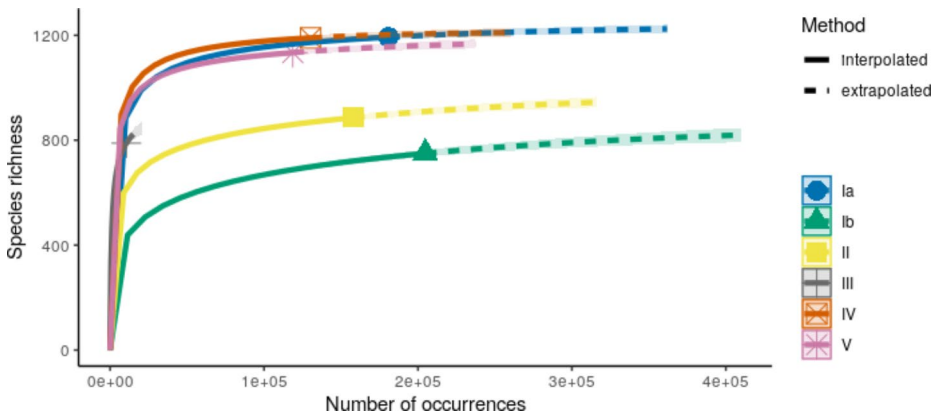
Fig. 3 Species accumulation curves (rarefaction curves with Hill numbers) within different types of protected areas in Fennoscandia, separated by IUCN categories: **Ia)** Strict Nature reserve, **Ib)** Wilderness area, **II)** National Park, **III)** Natural monument, **IV)** Habitat/Species management, and **V)** Protected Landscape. The x-axis shows the number of occurrences and the y-axis the species richness. Each protected area category has their own interpolated (solid) and extrapolated line (stippled), represented by different colours as specified in the legend

except for category V. Protected areas of category III with small size displayed low levels of diversity similar to the other categories, but no large-sized protected areas were present (max size: 19,61 km², Table S1). The slope of the species-area curves varied from 0.190 to 0.293, while the slope of the phylogenetic diversity-area curve varied from 0.120 to 0.186 (Fig. 4, Figure S7, Table S5). The proportion of PD represented in each category was higher and reached a higher value faster compared to SR (Fig. 4). For all categories we found that significantly more diversity can be found with a larger area (Table S5). Especially in small areas, no difference in between the different categories was visible.

Discussion

In this study, we investigated biodiversity patterns of vascular plants within protected areas across Fennoscandia, in terms of both SR and PD. There was a difference in SR and PD between unprotected and protected areas of the different countries (H1). We also observed differences in the patterns of SR and PD between the different types of protected areas, classified by the IUCN. Protected areas in categories II and V were higher in biodiversity than those protected areas classified as categories Ia, Ib and III (H2). Further inspection of these patterns using diversity-area curves demonstrated that PD reached higher values faster with increasing size than SR, and both measurements had higher values in larger protected areas (H3). This study highlights the importance of evaluating diversity in an area for establishing protected areas, and that land-use history influences placement of protected areas to the detriment of high diversity regions.

Spatial patterns in SR and PD in Fennoscandia were similar, with PD generally being higher than SR (when expressed as a proportion of the total diversity across the study region). These findings conform with expectations, since PD is dependent on SR, and with an increasing SR the range of distantly related species is greater (Figure S3, e.g., Brummitt
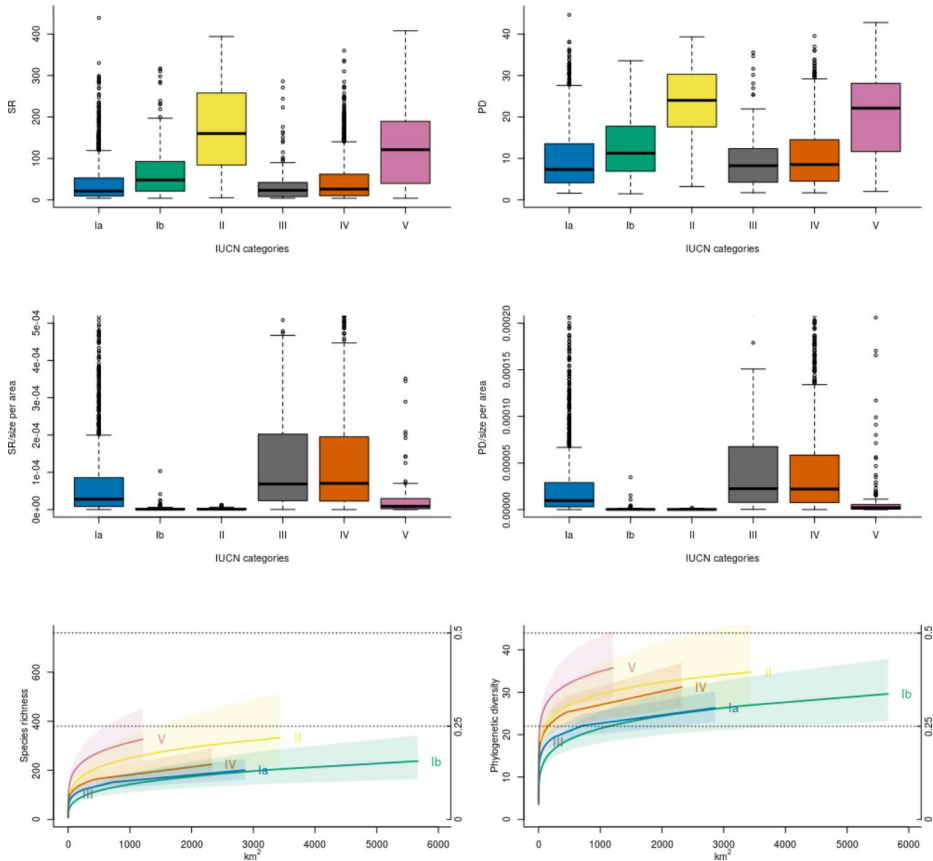
Fig. 4 Diversity area relationships of protected areas in Fennoscandia, comparing plant species richness (left) and phylogenetic diversity (right). The top row shows the unscaled diversity values and the second-row diversity scaled by area size (km²). The whiskers in the boxplots show the 95% confidence interval and the black line in the box the median, the dots falling outside the whiskers are outliers. The bottom row shows the predicted relationship between area and diversity displayed for the separate IUCN protected area categories, shaded areas represent the 95% confidence intervals and the right axis shows the proportion of the total of SR and PD. Colours correspond to the protected area categories, Ia: blue (Strict Nature reserve), Ib: green (Wilderness areas), II: yellow (National Park), III: black (Natural monument), IV: pink (Habitat/Species management), V: red (Protected Lanscape)

et al. 2021). Specifically, we observed the highest diversity (SR and PD) of vascular plants in the southern regions of all three Fennoscandian countries and along the coastline of Norway, and low diversity in the centre of Fennoscandia. Especially in Norway and along the western coastline we found phylogenetic clustering, while some phylogenetic overdispersion was found scattered in the northern parts. We found concentrations of long branches in the northern parts of Fennoscandia and a concentration of short branches along the southern coast of all three countries. A concentration of short branches can be found in the south, potentially indicating recent diversification (Mishler 2023).

These results are dissimilar in many ways to the findings of Mienna et al. (2020) who in a study including only Norway, found phylogenetic overdispersion along the western

coast of Norway, and some clustering in mountain and northern regions. This discrepancy between Mienna et al.'s (2020) Norwegian study and our Fennoscandian study highlights how diversity patterns are very sensitive to scale (Chase et al. 2019). This study of the whole Fennoscandian flora included more taxa and their spatial data, randomized across a wider geographic range than the Norwegian study, thus our results show broader-scale diversity patterns than those found in the Norwegian context, which are still correct looking at that scale only. Scale dependence of phylogenetic structure at various biogeographical scales has been shown to affect patterns (Mishler et al. 2020), due to relationships between species niches and habitats and how habitats distribute over space (Okuno et al. 2022). Few areas of phylogenetic clustering or overdispersion overlap with protected areas.

Few of the regions with short branch concentrations and phylogenetically clustered areas overlap with protected areas, long branch concentrations and phylogenetic overdispersion fall mostly outside of protected areas. A concentration of long branches can show long evolutionary history (Mishler 2023), while phylogenetic overdispersion can show evolutionary divergence (Cavender-Bares et al. 2004). In the centre of Fennoscandia (along the border between Sweden and Norway and Sweden and Finland) is region sparse in species occurrence data, with few individuals or institutions regularly reporting, which lead to localities being excluded from the analysis, due to the very few occurrences. The coastline is characterised by high habitat heterogeneity with deep fjords and steep mountains. Southern Fennoscandia represents more productive and warmer regions (Figure S4; Mienna et al. 2020), and show a concentration of short branches, indicating regions of potential differentiation (Mishler 2023). Southern regions generally support higher diversity compared to colder and less productive regions. In southern Fennoscandia a higher human population density is found, which induces a bias of specimen occurrence records (Speed et al. 2018). This increase in possible collection and recording may increase the estimates of diversity within the regions, where the opposite might happen in the centre of Fennoscandia. A higher population density also increases a roadside bias, a bias to collection closer to infrastructure (Petersen et al. 2021), with higher sampling in agricultural, developed areas and grazing lands (Pärtel et al. 2005). However, we did account for spatial autocorrelation and excluded ambiguously identified taxa, which should limit the sampling bias in space and across taxa. Hence, environmental conditions are a more likely explanation for the observed higher diversity, as we can also see on the patterns of NPP and temperature (Figure S4).

Worldwide the effective management of protected areas has been evaluated in only 18% of them, with differing objectives of effectiveness, making a universal statement of effectiveness inadequate (UNEP-WCMC and IUCN 2020). Since protected areas cover only around 15% of landmass in Fennoscandia (17% of Norway, 15% of Sweden and 14% of Finland, UNEP-WCMC and IUCN 2020), the unprotected regions contribute to long-term conservation of diversity. This has already been shown for Mediterranean ecosystems across several taxa of flora and fauna (Cox and Underwood 2011). Even though we found an overall higher diversity within unprotected areas across the countries of Fennoscandia, it is important to consider that these land masses do not represent one continuous large area, but highly fragmented pieces in the landscape, more so than protected areas. This gives not only a number of challenges but also opportunities to manage these areas to be beneficial for humans and ecosystems. A well-managed area surrounding a protected area for example can act as a buffer zone and make protected areas less vulnerable to changes (Hansen and DeFries 2007). However, ideally, protected areas should include higher diversity compared

to unprotected areas, as it would indicate their functioning as species refugia against the disturbance and habitat fragmentation usually seen in many unprotected areas. Here we are unable to conclude that the protected area management in Norway, Sweden, and Finland, positively affects biodiversity. Although it has been found that increasing effectiveness of existing protected areas decreases forest loss, which brings opportunities to improve the existing protected area network (Shah et al. 2021). Increasing effectiveness of existing protected areas might be more valuable than establishing new areas unless diversity is considered. Conservation areas are often established without measuring biodiversity, in favour of socio-economic factors rather than conservation features (Kusumoto et al. 2017). This also explains why most protected areas in Fennoscandia can be found at high elevations and latitudes, outside the most productive regions.

As expected, larger-sized protected areas generally contained more diversity (SR and PD) compared to protected areas of smaller size (Fig. 4). However, it is surprising that areas with the less strict protection category (V) have generally steeper diversity-area curves than the stricter protected areas (Ia, and Ib). This might be because of a collection bias, that the less-strict protected areas are used for recreational purposes and therefore can have a high number of records, whereas stricter protected areas are less accessible to the public, leaving the collection to the management of the areas. Since we accounted for a collection bias, the more likely reason lies in the location of the protected areas (Figure S1). Large and strictly protected areas are often located in mountainous and generally species poorer regions and the less strictly protected areas are often located in the southern and more productive regions. Even though the strictly protected areas (Ia and Ib) show a shallower increase of diversity with area size, the absence of human pressure cannot be underestimated, and it has been shown that these areas are under considerably lower human pressure, giving biodiversity a higher chance of persisting (Jones et al. 2018). Even in species poorer regions, diversity can increase substantially with area size, when the area size is large enough, which can be observed in the largest protected areas, the National Parks (II). Although even small areas, such as the protected areas of habitat/species management (IV) can have a steep increase of diversity with increasing area, this is likely due to the specific conservation objective of protecting specific species, groups, or habitats.

Taking diversity-area relationships into account can be valuable for conservation planning, and we show that taking area size into account leads to different results than not doing so. Since protected areas are more vulnerable in effectively protecting biodiversity when located closer to human land use and when they are smaller in size (Hansen and DeFries 2007), evaluating diversity-area relationships adds to the benefit of protected areas. Larger areas are also less susceptible to edge effects and species loss due to fragmentation. For example, the existence of roads close to protected areas has been shown to lead to a higher deforestation rate, which could be mitigated with stricter protection (Aguirre et al. 2021). Both SAR and PDAR can be used to predict SR and PD through habitat loss (Mazel et al. 2015). Losing PD at any scale reduces genetic diversity and, therefore, the potential for communities to change (Morlon et al. 2011). Since PD is highly correlated with SR, a steeper increase with area is expected with smaller area, although this is different for larger areas (Mazel et al. 2015), especially when using a measure of PD that is dependent on SR (Farneda et al. 2020). Adding a long-branched taxon will have a stronger effect on PD than on SR, which will be more noticeable in smaller areas, however our analysis highlights areas with concentrations of exceptional long or short branches and we found more areas

with short branches than long branches and overall little overlap of the latter with protected areas. Unlike SR, the increase of PD with area can give insights in assemblages and dispersal ability of species. For example, a steeper PD-area curve can be a sign that dispersal limitations were a driving evolutionary force resulting in a phylogenetic clustering (i.e. co-occurring species are closely related), especially at smaller scales (Morlon et al. 2011). A flatter PD-area curve (and no dispersal limitations) can result in phylogenetic overdispersion (i.e., co-occurring species are distantly related) at smaller scales. Fennoscandia was covered by the Fennoscandian ice sheet until 22–9.7 thousand years ago (Stroeven et al. 2016), and indeed, phylogenetic clustering has been found in the Norwegian mountains and the northern parts of Norway and phylogenetic overdispersion at the coastline (Mienna et al. 2020). Protected areas of category Ib overlap with a large part of the Scandinavian mountains and the north of Fennoscandia, which also has the steepest increase in the PD-area curve (Table S5). The flattest curve has protected areas of category V, which is mostly found in the southern parts of Fennoscandia, the part with the longest evolutionary history. Additionally, areas with high PD are likely to include more evolutionary history and therefore functionally diverse and resilient communities, thereby increasing ecosystem stability (Cadotte et al., 2011, 2012). Overall, our results suggest that protecting PD might bring higher benefits for conservation than SR over a small area. Other studies have found similar trends in other locations and species groups (Mazel et al. 2015; Morlon et al. 2011). Protecting biodiversity effectively includes a plenitude of facets, one way to protect more is to include PD in the planning stages.

Understanding patterns of plant diversity on a broader scale will help put local conservation action into context. Broad-scale studies are needed to make local conservation action work with the broad-scale patterns (Chaplin-Kramer et al. 2022). This study reveals broad phylogenetic and species diversity patterns within the distribution of northern European vascular plants and shows that the current protected area system in Fennoscandia does not protect the areas of high PD and SR. We also highlight that to increase effectiveness of already existing and new protected areas and to avoid protecting areas which do not contribute to biodiversity protection of vascular plants, conservation actions should take PD into account, especially on smaller scales and increase the focus on the location of protected areas.

Author contributions D.M.M., M.B., M.D.M., and J.D.M.S. conceptualised and designed the study. D.M.M analysed, visualised, and wrote the original draft. I.M.M., V.C.B., V.C.M., M.N. and K.E.M.V. contributed to data collection and laboratory work. All authors reviewed, edited, and approved the draft.

Data Availability Data generated and analysed in this study are available in the supplementary information or found in the following public repository. All newly generated sequences are deposited on Dryad (https://doi.org/10.5061/dryad.n8pk0p303); Species occurrence records: GBIF.org (24 July 2020) GBIF Occurrence Download – 24 July 2020 (https://doi.org/10.15468/dl.qvb7j8; https://doi.org/10.15468/dl.kpmkf3 and https://doi.org/10.15468/dl.wzp39d).

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Damaris M. Matten[1] · **Ida M. Mienna**[1,2,3] · **Vanessa C. Bieker**[1] · **Brent D. Mishler**[4] · **Victoria S. Moen**[1,5] · **Malene Nygaard**[1,6] · **Katariina E. M. Vuorinen**[1,7] · **Mika Bendiksby**[1,2] · **Michael D. Martin**[1] · **James D.M. Speed**[1]

✉ Damaris M. Matten
damaris.m.matten@ntnu.no

[1]   Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

[2]   Natural History Museum, University of Oslo, Oslo, Norway

[3]   Faculty of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway

[4]   University and Jepson Herbaria, Department of Integrative Biology, University of California, Berkeley, CA, USA

[5]   Norwegian Institute of Bioeconomy Research (NIBIO), Grimstad, Norway

[6]   Natural History Museum and Botanical Garden, University of Agder, Kristiansand, Norway

[7]   Norwegian Institute for Nature Research (NINA), NINA Lillehammer, Vormstuguveien 40, Lillehammer 2624, Norway