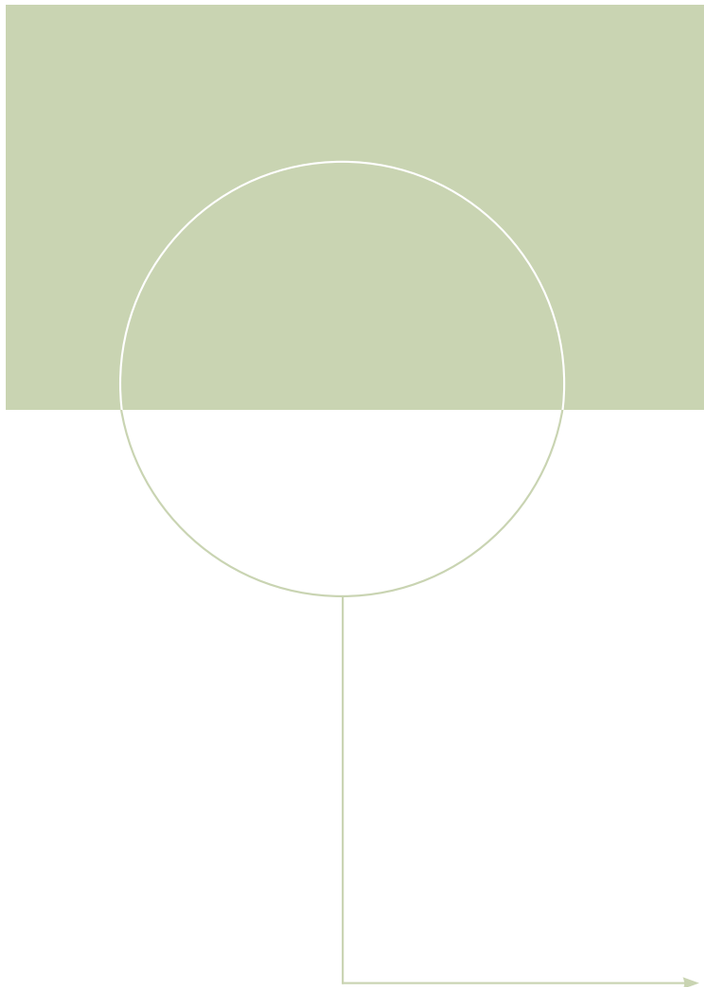

Master's thesis

2020

Kjersti Rønhovde Styve

NTNU
Norwegian University of
Science and Technology
NTNU University Museum
Department of Natural History

Kjersti Rønhovde Styve

Associations in Phylogenetic Diversity Patterns across Trophic Levels throughout Norway

June 2020

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of
Science and Technology

Associations in Phylogenetic Diversity Patterns across Trophic Levels throughout Norway

Kjersti Rønhovde Styve

Master's thesis in Natural Science with Teacher Education
Submission date: June 2020
Supervisor: James D. M. Speed
Co-supervisor: Damaris Matten

Norwegian University of Science and Technology
Department of Natural History

Abstract

This study investigates to what extent associations in phylodiversity (PD) exist between trophic groups in Norway. This was done by calculating the PD within communities delimited by grid cells of 20 x 20 km in mainland Norway, and subsequently compare their spatial patterns for different trophic group—producers, herbivores, invertivores, omnivores and carnivores. In addition, species richness (SR) were also calculated and mapped, to assess the correlation between PD and SR. A random distribution of the phylogenetic diversity was made, to locate and compare areas with higher or lower PD than expected by chance. This allowed investigation of patterns of PD after the effect of species richness is removed. Regression analysis were conducted to examine how PD covaried in space for the six trophic groups. The residuals for each of the fitted relationships were mapped, to analysis spatial variances in relationships of PD between trophic groups. The results of the study found significant, positive correlations in PD between all the trophic groups, and further a high degree of correlation in SR and PD throughout Norway.

Sammendrag

Denne oppgava har som hensikt å undersøke om det eksisterer sammenhenger i fylogenetisk diversitet (*phylogenetic diveristy; PD*) på tvers av ulike trofiske grupper i Norge. PD ble beregnet i ulike samfunn, hvor hvert samfunn ble definert av de artene som befant seg innenfor områder på 20 x 20 km i Fastlands-Norge. PD ble beregnet separert for hver av de ulike trofiske gruppene—produsenter, herbivorer, invertivorer, omnivorer, granivorer og carnivorer—før verdiene for PD ble projisert for å kunne sammenligne den romlige fordelingen av PD på tvers av gruppene. Artsrikheten (*species richness; SR*) ble også beregnet for å kunne bestemme sammenhengen mellom PD og SR. En romlig randomisering av PD ble gjort, for å kunne lokalisere og sammenligne områder med statistisk høyere eller lavere verdi enn forventet, samt undersøke den romlige fordelingen av PD uten påvirkning fra SR. Videre ble regresjonsanalyser benyttet får å undersøke sammenhengen i PD mellom de ulike trofiske gruppene ytterligere, før avvik fra sammenhengen ble projisert, for å kunne analysere den romlige variasjon. Resultatene viste signifikante, sterke korrelasjoner mellom mønstre av PD på tvers av de trofiske gruppene, i tillegg til sterk korrelasjon mellom SR and PD i de definerte samfunnene i Norge.

Acknowledgements

First and foremost, I would like to thank my two wonderful supervisors, James D. M. Speed and Damaris Matten, for their invaluable guidance and help throughout the whole project, in addition to gathering necessary data used in this study. I would also like to thank my friends and family for their support, and especially my mum and Jorunn for always believing in me.

Writing this thesis has provided me with deeper insight into the field of macroecology, increasing my knowledge about community structures, drivers of diversity and trophic interactions, which is of great values as future biology teacher.

Table of contents

List of abbreviations

PD Phylogenetic diversity

SR Species richness

rPD relative phylogenetic diversity

1. Introduction

1.1 Background

Spatial variation of biodiversity can be seen as the product of events of speciation, extinctions and dispersal through time (Cadotte & Davies, 2016; Swenson, 2011). To understand the underlying ecological and evolutionary processes that have influenced biodiversity patterns through space and time, is thought to be one of the main goals of ecologists and evolutionary biologists (Swenson, 2011). Today, the goal of studying biodiversity is not only to aid understanding of patterns of species distribution, but also to understand how to best preserve and protect it (Primack, 2014), as loss of biodiversity through species extinctions is documented world wide (e.g. Ceballos et al., 2015; Wake & Vredenburg, 2008).

Traditionally, the quantification of biodiversity has been centered around species diversity in terms of species richness (hereinafter referred to as 'SR') (MacArthur, 1965; Wiens & Donoghue, 2004). The prevalent use of SR as proxy for biodiversity has been criticized for presenting a simplified picture of biodiversity, since it does not take differences in species ecology and evolutionary history into consideration (Safi et al., 2011; Swenson, 2011). Integration of phylogenies—the evolutionary relationships between focal species—into the study of species distribution and community assembly, supplement the understanding of patterns of biodiversity (e.g. Mishler et al., 2014; Wiens, Pyron, & Moen, 2011) by describing biodiversity as something more than the number of species present within a community.

A biodiversity metric that gives weight to the evolutionary distinctiveness of species, is phylogenetic diversity (Kling, Mishler, Thornhill, Baldwin, & Ackerly, 2019). Originally introduced as a tool for conservation biology (Faith, 1992) it allows the quantification of evolutionary relationship between species within a community. Accordingly, it allows identification of evolutionary distinct species and adds to recognition of areas in most need of protection. Following the definition by Faith (1992), phylogenetic diversity (hereafter referred as 'PD'), is the sum of branch lengths that connect all species within a community together. PD has a tendency to be highly correlated to SR, as shown for several taxa (Fergnani & Ruggiero, 2017; Fritz & Rahbek, 2012; Voskamp, Baker, Stephens, Valdes, & Willis, 2017). However, integration of phylogenies still adds to biodiversity analyses by other means; identifying and analyzing sites with deviations in PD, can help identifying important drivers and mechanisms that underpin community assembly and create and maintain biodiversity (Pavoine & Bonsall,

2011; Safi et al., 2011). This sort of analysis can be conducted through different methods, for example by comparing observed values of PD against expected values of diversity provided from null modeling of random species co-occurrence (Cadotte & Davies, 2016).

Prior studies have investigated the phylogenetic structure of communities, and detected patterns of phylogenetic clustering and overdispersion (see Emerson & Gillespie, 2008). A phylogenetically clustered community is defined by closely related species which co-occur more frequently than expected, whilst an overdispersed community has species that are more distantly related than expected (Johnson & Stinchcombe, 2007). Much of the research that has investigated the phylogenetic structure within communities, have seen patterns of phylogenetic clustering and overdispersion as the results of two contrasting processes; namely environmental filtering and competitive exclusion, respectively (Emerson & Gillespie, 2008; Webb, Ackerly, McPeek, & Donoghue, 2002).

Environmental filtering can generally be defined as the process where a set of environmental conditions are believed to select for certain traits which an organism must possess to survive and persist within a given habitat (Emerson & Gillespie, 2008; Johnson & Stinchcombe, 2007). This set of traits have a higher possibility of being shared among closely related species, due to common descent and the tendency of phylogenetic niche conservatism (Cadotte & Davies, 2016; Johnson & Stinchcombe, 2007). Consequently, studies detecting phylogenetic clustering is commonly interpreted as evidence for environmental filtering (Mayfield & Levine, 2010). Phylogenetically clustered communities are commonly associated with high-stress environments where climatic and anthropogenic elements function as environmental filters (e.g. colder temperatures and disturbance) (Cadotte & Davies, 2016; Elton, 1946).

The competitive exclusion principle generally states that two species with identical niches (i.e. competitors) cannot coexist over longer periods of time in a stable environment (Begon, Townsend, & Harper, 2006). Awareness of the ability of competition to affect community assembly is not recent, and has been widely recognized within ecology. Darwin (1859) remarked that closely related species tend to be ecological similar, and hence will compete more severely than distantly related species. Sharing of traits between close relatives and the tendency of niche conservatism, closely related taxa will be each others' strongest competitors, and thus competitive exclusion is thought to prevent closely related taxa from co-occurring (Webb et al., 2002). Accordingly, competitive exclusion is generally thought to

be a driver of phylogenetic overdispersion in communities (Johnson & Stinchcombe, 2007). Nevertheless, Mayfield and Levine (2010) argue that competition can also be a driver of phylogenetic clustering, if traits that are phylogenetically conserved enhance species competitive ability, which can result in a clustered community with close relatives that are superior competitors, and hence outcompete more distantly related species.

Drivers of the phylogenetic structure of a community have been investigated for various taxa. Voskamp et. al (2017) assessed large scale patterns in the distribution of terrestrial birds by locating regions with high and low values of relative phylogenetic diversity (rPD; in relation to what expected from SR). For the Palearctic (including Norway), stability since the last interglacial period was the most important predictor of rPD. Further, they showed that northern parts of the palearctic were one of the areas with the most negative rPD, globally. Voskamp et al. (2017) argue that low rPD could be the result of past glaciation coverage under Last Glacial Maximum (LGM), causing climatic fluctuations and hence these areas more prone to events of local extinctions which could ultimately have led to areas of relatively underdeveloped fauna, in terms of few old lineages. A similar study by Safi et al. (2011) on terrestrial mammals, showed that PD were related to evapotranspiration (i.e. productivity) and that it increased relative to SR with increasing mean annual temperature.

The spatial patterns of PD differ between mammals, birds, and amphibians in Europe (Zupan et al., 2014). While relatively high values of PD were found for mammals and in European mountains, the opposite were found for birds (i.e. negative rPD). In addition, birds had high rPD in areas close to rivers and lakes, which were not found for the remaining vertebrates. This is in accordance with the results from Voskamp et al. (2017), who found low rPD in birds in mountainous areas. Additionally, birds are commonly found in isolated areas and islands, which is not the case for amphibians (Fritz & Rahbek, 2012) nor mammals (Davies & Buckley, 2011).

It is well known that interactions among species, such as competition and predation can be important determinants of SR (Cadotte & Davies, 2016). Nevertheless, such biotic factors have been argued to be a driver for the distribution and assemblage of species only at local scales (e.g. Pearson & Dawson, 2003) and following that large-scale processes, such as climate, accounts for shaping the distribution and species assemblages at broader spatial extents. By contrast, studies reported by Wisz et al. (2013) conclude that biotic interactions indeed have

influenced the distribution of species and their assembling into communities at broad scales. This conclusion is in accordance with the results from Sandom et al. (2013), which indicates that predator-prey interactions in mammal species can drive SR gradients on a global scale.

In literature, it has been documented how diversification and speciation within prey species can have cascading effects throughout the food web, and hence drive evolution among interacting species at higher trophic levels (Brodersen, Post, & Seehausen, 2018). In terrestrial food webs, plants generally compromise the lowest level of resources, and studies have shown how the genetic diversity within plants structures and supports specific arthropods communities (e.g. Johnson & Agrawal, 2005) and may indirectly affect species on higher trophic levels (Bailey, Wooley, Lindroth, & Whitham, 2006), given genetic correlations between plant traits and associated communities.

Various literature has studied the phylogenetic distributional pattern in context of trophic interactions. Speed et al. (2019) studied drivers of diversity patterns within communities of Arctic vertebrate herbivores and found that phylogenetic diversity increased with both bottom-up and top-down interactions, using vegetation productivity and predator SR as proxies, respectively. In addition, winter minimum temperature, used as proxy for environmental harshness, was the most important abiotic factor associated with phylogenetic diversity, resulting in a pattern where areas experiencing colder winters, having a higher phylogenetic diversity. This is perhaps counterintuitive, given that climate severity often is seen as a limiting factor of taxonomic diversity, with cold or dry environments having less taxonomic richness than 'milder' environments (Currie et al., 2004). Speed et al. (2019) argue for several possible explanations, among others that vertebrates are able to follow multiple colonization pathways to the high-latitude areas within the Arctic, as seen for plants (Alsos et al., 2007).

The spatial pattern of SR and phylogenetic diversity of Norway's native vascular plants have been investigated (Ida M Mienna et al., 2020). The distribution of SR and PD among the vascular plants, were similar in terms of location of areas with the highest and lowest values of diversity. Both metrices had highest values along the coastline of Norway, but only in the southern parts. It was also in these parts of the country that areas with significantly high PD (i.e. phylogenetic overdispersion) were located. In contrast, diversity deficient areas were found in the northern parts and at high-altitudes levels, together with areas with significantly low PD (i.e. phylogenetic clustering). Important drivers of spatial patterns of PD and SR were found to

be of mainly bioclimatic matter; both SR, PD, and overdispersion increased with habitat heterogeneity and summer temperatures, while the opposite was true for clustering. Time since last glaciation was positively correlated with phylogenetic overdispersion, and negatively correlated with phylogenetic clustering.

Allegedly, temperate areas have less species diversity than the tropics, because frequent disturbances through time, such as glaciations during the Pleistocene, have hindered these areas to reach closer to saturation and fully exploitation of resources (Begon et al., 2006). Regions that were not covered by ice during LGM, such as the southern peninsulas in Europe, worked as ice age refugia, and species from here dispersed into and recolonized Europe through distinct colonization pathways (Hewitt, 1999). Norway was fully covered under the Scandinavian ice sheet during the peak of the most recent glacial period (LGM, 26.5-20 thousand years ago)(Clark et al., 2009) and as a consequence, the fauna and flora of Norway is characterized by species that colonized the mainland after the glaciers started retreating, and can be categorized as a region which have had relatively short time to support speciation events.

1.2 Objectives and hypotheses

The main aim of this project was to examine associations in PD across trophic levels in Norway. In addition, the general relationship between SR and PD was assessed.

It was hypothesized to find positive associations in patterns of phylogenetic diversity across the trophic groups included in the study (H_1). In addition, producers were expected to have higher values of PD relative to the other trophic groups in coastal areas, due to better dispersal abilities in plants (H_2). Finally, it was expected that areas with high PD in producers, would have corresponding high PD in invertivores (H_3).

2. Methods

2.1 Selection of species and retrieval of distributional data

The four classes of animals included in this study were birds (209 species), mammals (49 species), amphibians (6 species) and reptiles (5 species). Distributional data was obtained from various online databases, with species being limited to include resident, terrestrial vertebrates. All obtained species lists were cross-referenced with The Norwegian Red Lists provided by The Norwegian Biodiversity Information Centre (Henriksen & Hilmo, 2015) in order to verify their belonging in the Norwegian fauna. No livestock species were included.

The distributional data of the mammals was obtained from the IUCN Red List database (International Union for Conservation of Nature) (IUCN, November 2019). The list of mammalian species was filtered to included extant and resident species, in accordance with the list provided by Artsdatabanken. One species (*Pipistrellus pipistrellus*) was missing from the spatial data, due to its range not covering Norway in the data obtained from the IUCN database.

The avian distribution maps were constructed using spatial data from BirdLife International (2016). The maps were cropped to only include those species that overlap with the extent of Norway, containing both species classified as introduced and vagrant, in addition to the native ones. The assessed list of 250 species was compared to the Norwegian Red Lists that only include species that are established and regularly breeding in Norway, leaving a total of 224 native species. This excludes six species which were not part of the original distribution data provided by Birdlife, including among others the hooded crow (*Corvus cornix*), which is considered one of the most widespread bird species in the Norwegian fauna.

Species distribution maps for amphibians and reptiles were collected from the updated atlas of amphibians and reptiles of Europe from Societas Europaea Herpetologica (Sillero et al., 2014). A total of 6 amphibians and 5 reptiles are included in this study, in accordance with Dolmen (2008) and the Norwegian Red List (Henriksen & Hilmo, 2015).

Finally, the spatial data for plants were obtained from The Global Biodiversity Information Facility (GBIF) based on the methods and criteria used by Ida Marielle Mienna (2018). Due to the use of updated occurrence data from GIBF, this analysis included only 1 118 vascular

species, out of the 1 238 vascular species included in Mienna's study (see Ida Marielle Mienna, 2018).

2.2 Trait data and phylogenies

Information about the diet and foraging stratum for birds and mammals were collected from the trait database EltonTrait (Wilman et al., 2014), which provides percentage estimates of a species diet within 10 different diet types. These types were merged to 5 main categories namely (1) invertebrates, (2) plants, (3) seeds, and (4) vertebrates. The EltonTraits (2014) also contains information about forage stratum, which were used to remove birds species that are pelagic, leading to the removal of additional 15 birds from the distribution set.

All species were classified into one of six trophic groups, namely producers, herbivores, granivores, invertivores, carnivores and omnivores (table 1). These trophic groups represent several trophic levels within an ecosystem, and each of them were defined by a set limit of how much of a species' diet belonged to one of the abovementioned diet categories (see table 1). Trait data for amphibians and reptiles were obtained from literature (Fog, de Lasson, & Schmedes, 1997), and were categorized into a trophic group based on a qualitative description of their diet, where terms like 'mostly' and 'mainly' were understood as equal to >50% of a given diet (e.g. a reptile that 'feeds mainly on rodents' were categorized as carnivore).

Table 1. Number of species within the trophic groups of consumers according to their diets provided by EltonTraits (2014) and Fog et al. (1997).

Trophic group	Diet	No. of birds	No. of mammals	No. of amphibians	No. of reptiles
Herbivore	$\geq 70\%$ plants	14	11	-	-
Granivore	$\geq 70\%$ seeds	4	-	-	-
Invertivore	$\geq 50\%$ invertivores	108	16	6	2
Carnivore	$\geq 50\%$ vertebrates	33	8	-	3
Omnivore	$< 70\%$ plants & $< 70\%$ seeds & $< 50\%$ invertivores & $< 50\%$ vertebrates	50	14	-	-

The phylogeny for the producers were obtained from the work of Ida Marielle Mienna (2018), and is a non-ultrametric tree that captures different lengths of evolution. The phylogeny was trimmed by using the *picante* package (S. W. Kembel, Cowan, P.D., Helmuus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010) to only include 1 118 included branch tips (i.e. species). The phylogenetic tree for animals, were constructed using the online *TimeTree* resource (Kumar, Stecher, Suleski, & Hedges, 2017) which returned an ultrametric tree scaled to divergence times, with a total of 269 branch tips. This excludes 1 species *Muscicapa striata*, which were not found in the TimeTree-database.

2.3 Analysis of biodiversity

All the distributional data, except amphibians and reptiles (which were provided as grid maps), were originally obtained as polygon layers, which were rasterized into 20x20 grid cells and projected to the same coordinate system (WGS84/UTM zone 32N) using the packages *sp* (Bivand & Pebesma, 2005) and *fasterize* (Ross, 2020). The distributional data for plants were used as template for making the remaining groups. Resulting in presence-absence rasters for each species with 1 102 grid cells.

The distribution layers of all species were used to build different datasets, in order to make separate maps depicting diversity for each trophic group (producers, herbivores, granivores, invertivores, omnivores and carnivores) and for each of the taxonomical group (plants, amphibians, birds, mammals and reptiles. In addition, a set of the combined values for all animals were made, to assess the relation between SR and PD for plants and animals separately, leaving altogether 11 species distribution data sets.

From these 11 data sets, maps depicting the value of SR and PD, both the actual values and the ratios of total diversity, were made. The two different diversity metrices, species richness (SR) and phylodiversity (PD), were calculated within each grid cell. SR was calculated as the sum of different species per grid cell. PD, i.e. species relatedness, was calculated by summing the total branch lengths connecting the species occurring in each grid cell (Faith, 1992), including the root of the tree. Additionally, climatic data and a map of Norway was downloaded from the package raster (Hijmans, 2019) and projected to WGS 84/UTM zone

32. The map of Norway was used as outline for the different maps, while the climatic data were used to add to the discussion.

The degree of correlation in spatial patterns of PD between the trophic groups was quantified by calculating Pearson's correlation coefficient, r, between PD of all groups. The statistical significance of correlation was included, with an alpha threshold of 0.05. Linear regressions on PD were performed on pairs of trophic groups, to identify the strength of the relationships between various groups, and to recognize deviations in the presumed relationship by mapping the residuals from each regression.

The statistical significance of the observed spatial patterns of PD was assessed by comparing the observed values of PD with the expected values provided by a null model randomization (Swenson, 2014). The null model randomization was done by using the *ses.pd* function, from the *picante* package (S. W. Kembel et al., 2010). Following this, areas with higher or lower values of PD than expected by chance, were recognized for the different trophic groups. The null model algorithm goes through each grid cell (i.e. community or assemblage) and reassigns species randomly from the species pool to it. This is done with all grid cells, keeping the SR within each grid cell constant. The whole process was replicated 999 times to generate a null distribution and calculates p-values for each grid cell. A two-tailed test, using $p = 0.05$ as alpha level, was used to identify cells with a significantly higher (i.e. > 0.975) or lower (i.e. < 0.025) observed PD compared to the null distribution. Spatial randomization of producers was not conducted in this study, instead the map from Ida Marielle Mienna (2018) was used. All analysis were conducted in *R* (R Core Team, 2019).

3. Results

3.1 Patterns of species richness and phylogenetic diversity

The observed spatial distribution of SR within each of the 6 trophic groups (producers, herbivores, granivores, omnivores, invertivores and carnivores) (figure 1a-f) show similarities in their distribution throughout Norway.

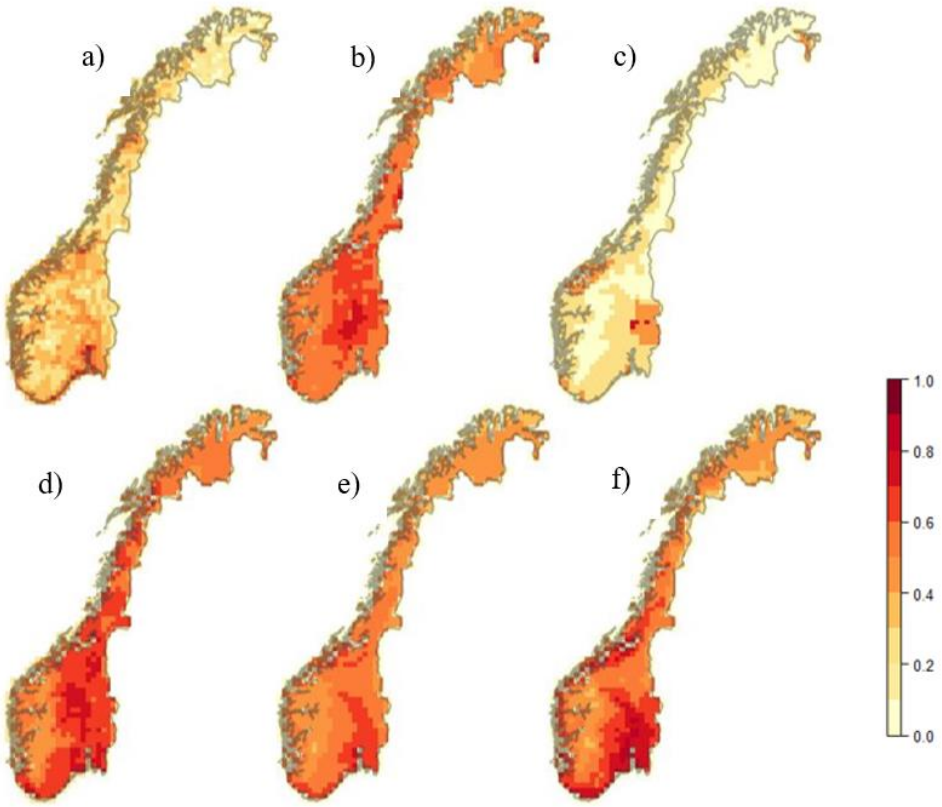

Figure 1. Distribution maps of species richness of (a) producers, (b) herbivores, (c) granivores, (d) carnivores (e) invertivores, and omnivores (f). WGS 84 / UTM zone 33N. All values are presented as proportions of the total number of species within each trophic group.

For all trophic groups, areas with high values of SR ($>60\%$ of the total number of species within their trophic group) are primarily found in the southeastern parts of Norway, with Oslo and adjacent areas being particularly rich. By contrast, areas in the northern and western parts of Norway generally have lower values of SR. Particularly low values of richness are primarily found along the coastline of Norway ($\leq 30\%$ of total SR). The richness pattern of granivores (figure 1c) have noticeable large, continuous areas with low SR ($\leq 30\%$). However, it should be noted that the granivores consist only of 4 bird species (table 1), hence those results should

be interpreted carefully. By contrast, the producers (figure 1a) have a more heterogeneous pattern than the other maps, which could be caused by the high number of different plant species, relative to the other trophic groups (see table 1).

Combining the spatial data with the phylogenies result in maps that show the distribution of phylogenetic diversity within each of the abovementioned trophic groups (figure 2a-f).

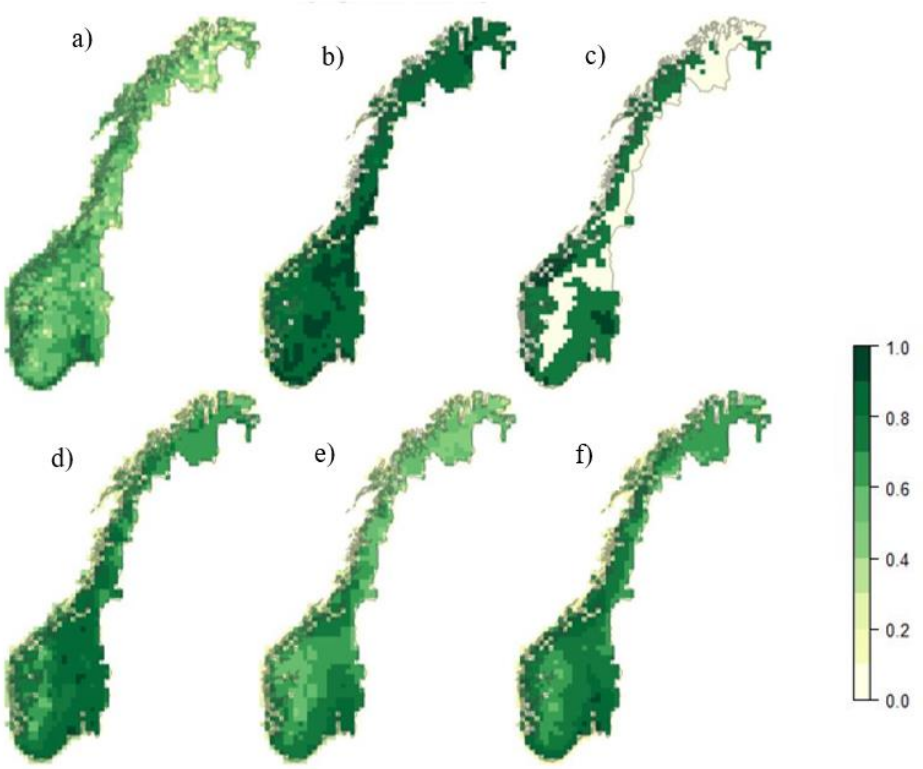

Figure 2. Distribution maps of phylogenetic diversity of (a) producers, (b) herbivores, (c) granivores, (d) carnivores (e) invertivores, and omnivores (f). WGS 84 / UTM zone 33N. All values are presented as proportions of the total amount of branch length within the specific trophic group.

Comparing the distribution of SR (figure 1) and phylogenetic diversity (figure 2), reveals a close similarity in their distribution patterns within the different trophic groups. Like SR, areas with higher phylogenetic diversity, i.e. higher taxonomical spread, are largely found in the southern parts of Norway (>70% of the total branch length within the respective group). Again, areas along the West Coast are characterized by low phylogenetic diversity (i.e. low taxonomical spread) and contain areas with < 30% of total branch length. Areas up north tend to have lower phylogenetic diversity, but this pattern is perhaps mostly apparent in producers, granivores and carnivores (figure 2a, 2c and 2e, respectively). As pointed out for SR, the

granivores and producers show distinct patterns also in the distribution of phylogenetic diversity. The pattern of granivores is dominated by large areas with low diversity ($\leq$ 10%) in mountainous areas in the south, up to the northern parts along the border to Sweden, and the producers show a more heterogenous pattern than the others.

The correlation coefficients were calculated to quantify the association between SR and phylogenetic diversity. Indeed, phylogenetic diversity shows a positive correlation with SR for both the producers figure 3a) and for the combined values for the animals (amphibians, birds, reptiles and mammals)(figure 3b), with correlation coefficients of $r = 0.96$ and $r = 0.98$, respectively.

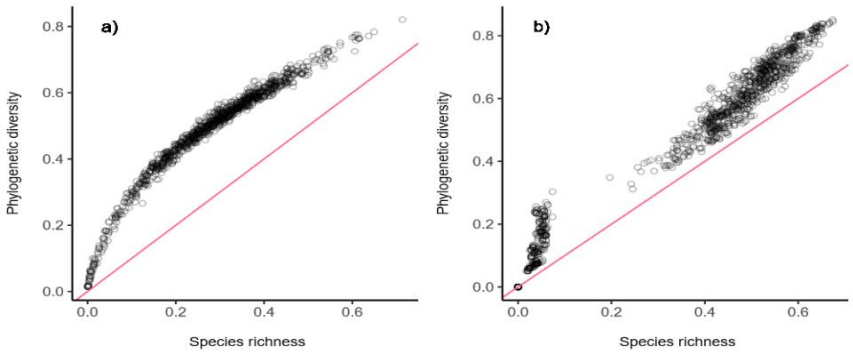

Figure 3. Correlation between species richness and phylogenetic diversity for (a) producers (r = 0.96) and (b) the combined values for amphibians, birds, mammals, and reptiles (r = 0.98). The red line illustrates a 1:1 relationship between phylogenetic diversity and species richness.

A positive correlation between SR and phylogenetic diversity is as expected, given the fact that addition of a new species into a community, will add extra branch length to the phylogeny as well. The noticeable splitting of points into two groups in the plot for the animal classes (figure 3b), is caused by only some mammals and birds apperaing in the small islands along the coast (see maps of SR in figure A2, appendix A).

3.2 Associations in phylogenetic diversity

Visually comparing the maps in figure 3, there appears to be some degree of association in phylogenetic diversity between the different trophic groups, most noticeable between carnivores, invertivores and omnivores (figure 3d-f), with some patches of lighter areas in the mountainous areas in the south west, a yellow lining at the west coast and darker areas in south east (indicating low and high values of phylogenetic diversities, respectively), following the general pattern described above. The producers (figure 3a) and herbivores (figure 3b) are expected to have a high degree of correlation, but this predicted similarity is not that clear by comparing their maps. The producers and herbivores also differ to some extent from the rest of the maps, making it harder to assess their degree of associations both to each other and the other groups by visual inspection.

The described associations between the different trophic groups are supported by the calculated correlation coefficients, which are presented in figure 4. Granivores were excluded from this and forthcoming analysis due to a low number of species.

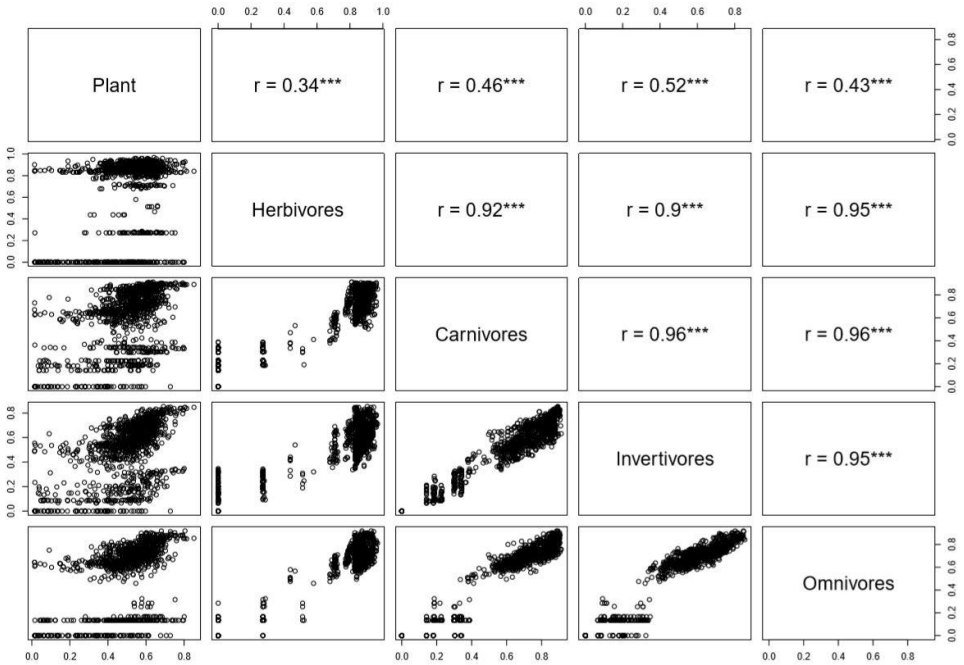

Figure 4. Results from correlation analysis of phylogenetic diversity between given trophic levels. The resulting correlation coefficient (r) between each of the trophic groups, is shown together with an asterisk that indicates the level of significance (*** = $p < 0.001$). All values are presented as proportions of the total number of species within each trophic group.

The degree of correlation (r) varies considerably between the different trophic groups, ranging from 0.34 to 0.96. As predicted by the visual interpretation of associations between trophic groups, the highest degree of correlation is found between carnivores and invertivores (0.96), carnivores and omnivores (0.96) and invertivores and omnivores (0.95). High degrees of correlation are also found between herbivores and the foregoing trophic groups (from 0.92 to 0.95), except the producers, which herbivores have a relatively low correlation with (0.34). In fact, the producers appear to have somewhat low correlations with all the trophic groups (ranging from 0.43 to 0.52). It should be noted that correlation plots with producers at the x-axis have a lot of values that appear close to 0, which are the result of areas only having a few plant species, which will show as values close to zero due to the high number of different plant species (1118 species).

3.3 Plotting of residuals and spatial randomization of phylogenetic diversity

The relationship in phylogenetic diversity between trophic groups was further investigated by plotting the residuals from regressions between certain trophic groups (explanatory variable/ response variable); producers~herbivores, producers~omnivores, producers~invertivores, herbivores~invertivores, herbivores~carnivores and herbivores~omnivores (figure 5a-f, respectively).

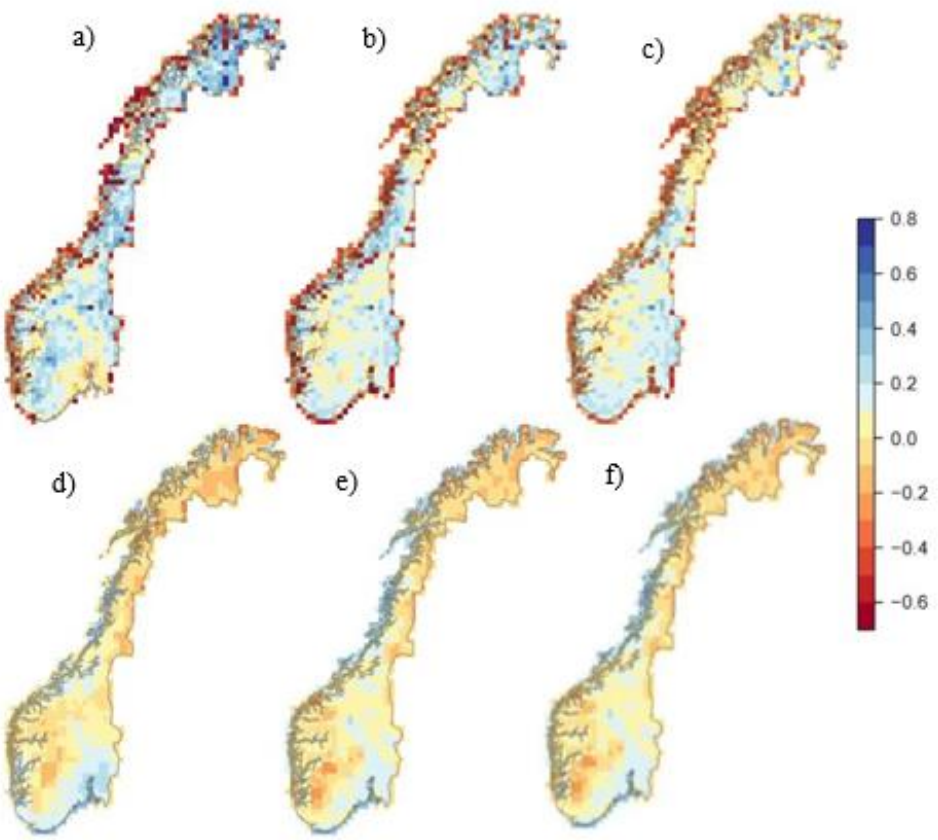

Figure 5. Residuals from linear regression of phylogenetic diversity between (a) producers~herbivores, (b)producers~omnivores, (c) producers~invertivores,(d) herbivores~invertivores, (e) herbivores~carnivores and herbivores~omnivores (f) . WGS 84 / UTM zone 33N.

The positive residuals (blue) show areas with *higher* PD within the given trophic group than expected, while the negative residuals depict areas with *lower* PD than expected (red). All regressions with producers' PD as explanatory variable (map a-c), share a number of key features; areas with negative residuals are located along the coastline and border to Sweden, while positive residuals are found scattered throughout northern and southern Norway. For regressions with herbivores' PD as explanatory variable (map d-f), positive residuals are found at Sørlandskysten and areas around Oslo, and to some degree in at the coast in mid-Norway.

The spatial randomizations of phylogenetic diversity (figure 6 a-d) show some noticeable differences from the observed phylogenetic diversity (figure 2a-f) and varies considerably in the number of significantly high or low values of phylogenetic diversity.

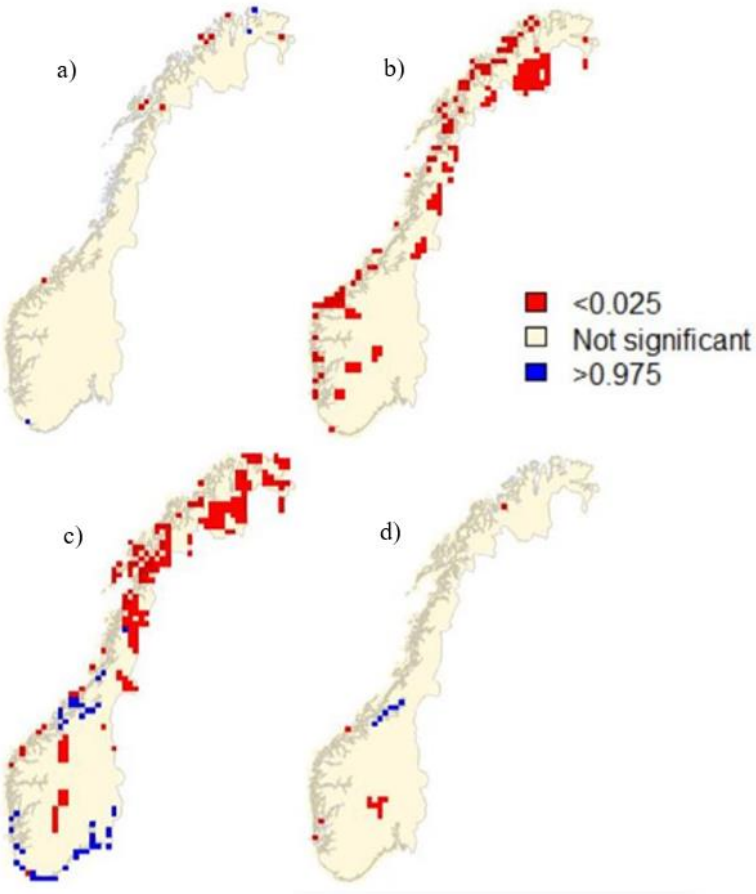

Figure 6. Results of spatial randomization of PD. Blue cells show areas with significantly high PD (>0.975) and red cells show significantly low PD (< 0.025) of a) herbivores, b) carnivores, c) invertivores and d) omnivores.

Both herbivores (figure 6a) and omnivores (figure 6d) have very few areas with diversity values that are significantly different from what is expected by chance. Carnivores (figure 6b) only have areas with significantly lower diversities than expected, which are in northern areas and at the West coast. Invertivores (figure 6c) have several areas of both significant high and low diversity, with high values of diversity found mainly in along the coast in southern Norway, and low values found in the north and in mid-Norway.

4. Discussion

4.1 Relationship between species richness (SR) and phylogenetic diversity (PD)

The observed distributional pattern of phylodiversity closely resembled the patterns of observed species richness, as expected. The visual interpretation of their resemblance was supported by a strong, significant correlation found between species richness and phylodiversity in both plants ($r = 0.96$) and animals ($r = 0.98$). These results are in accordance with similar studies on correlations between biodiversity matrices in various taxa (Fritz & Rahbek, 2012; Voskamp et al., 2017). The high degree of correlation is a consequence of the mathematical properties of the respective measures (Schweiger, Klotz, Durka, & Kühn, 2008), and from a biological perspective it is reasonable that addition of a new species to a assemblage or community nearly always will add a new branch to the phylogeny as well.

PD and SR show a linear relationship for animals, while the relationship in PD and SR for plants seem to be between linear and quadratic (figure 2). A possible explanation for the pattern observed for animals is that in a community with few species, it is more likely that addition of new species will add new phylogenetic information (i.e. PD) into the community, whereas in species rich communities, it is likely that the phylogeny have been well sampled already and that added species will not affect the PD considerably (Zupan et al., 2014). It is also worth noticing that PD in both plants and animals generally have higher values than SR across Norway. This could imply that the investigated communities in Norway tend to be overdispersed, i.e. more distantly related than expected from SR.

The displaying of the relationship between SR and PD in animals (figure 2b), reveals a split of the species into two separate groups. This is probably caused by low values of species richness found for animals in general along the coast of Norway (figure A2, appendix A). Especially for mammals and birds, there are a distinct difference in species richness when comparing the coastline areas and areas further away from the coast. For mammals, it seems to be on average less than 10 % of total SR along the coast, while the remaining mainland have values represented within a range of 45-80 %. A possible cause for this pattern could be that many of the larger mammals (e.g. *canis lups, gulo* and *ursus arctos*)(see table A1, appendix A) are restricted from the many islets found along the coast, leaving mainly small mammalian species such as *Mustela erminea* and *Mus musculus* (see table A1, appendix A) to occupy the coastal areas. These relatively small mammalian species are generally distributed along the rest of the

country, resulting in a split in the distribution data of mammals into two groups, with either low or high values of species richness (figure A2, appendix A). Additionally, the birds also have very few species along the coast (approximately 20 %) in contrast to the inland of Norway (40-70 %) (figure A2, appendix A). This observed pattern is probably caused by the exclusion of pelagic bird species in this study.

4.2 Associations in phylogenetic diversity (PD) between trophic groups

The main aim of this project was to examine associations in PD between trophic levels, and it was hypothesized that there would be positive associations in patterns of phylogenetic diversity between the trophic groups included in this study (H_1).

Surprisingly, the weakest correlation was found between producers and herbivores, both in values of PD (r = 0.34) and SR (r = 0.33). These findings were unexpected, as the cascading effects of diversification is thought to be stronger between subsequent levels in a food web (Brodersen et al., 2018) and since the structuring effects of plant genetics are demonstrated to act on herbivores directly, and have indirect effects on higher trophic levels (Bailey et al., 2006; Johnson & Agrawal, 2005). Still, the secondary consumers (omnivores, invertivores and carnivores) had substantially higher degrees of correlation with plants compared to the correlation between herbivore and plants, with values ranging from 0.43 to 0.52 (figure 4). These results all together provide support to the first hypothesis (H_1).

Associations between producers and higher trophic levels

Visually comparing the spatial distribution of PD between producers and herbivores (figure 1), it is apparent that they have some divergences in their distribution of PD. For example, herbivores have quite low values of PD in the coastal areas, while producers have relatively high values in the same areas. These results support our second hypothesis (H_2), which predicted a spatial mismatch between producer and animal PD in coastal areas. There are several possible explanations for this result. Plants commonly have the ability to disperse over long distance by wind and sea currents (Renner, 2004), enabling them to reach the Norwegian coast through multiple colonization pathways. Additionally, it is reasonable to assume that the great dispersal abilites allowed plants to recolonize the uncovered landmasses after the ice retrieved relatively fast compared to animals, hence possibly giving plants more time to speciate and diverge (Wiens & Donoghue, 2004). Indeed, Mienna (2018) found that vascular plants in

Norway were phylogenetically overdispersed in Norway's coastal areas, and this was related to the areas longer post-glacial history (see figure A3, appendix A).

Contrarily, the low values of PD for herbivores along the coast could be attritbuted to the low number of mammalian and bird species found in these areas (figure A2, appendix A), which are the only taxonomic groups part of the herbivores in this study (table 1). Nevertheless, comparing the overall distribution of PD in these two groups, herbivores tend to have relatively high values of PD (ranging from approximately 60-100 %) compared to plants (generally less than 70 %). This could imply that the examined herbivores are generally distantly related (i.e. phylogenetically overdispersed), which has been observed for vertebrate herbivores in the Arctic (Skjelbred, 2017). Then again, herbivores had very few areas where the observed PD were significantly higher than expected by chance (figure 6a), so rather then interpreting the high general PD in herbivores as indication of phylogenetic overdispersion, it could be caused by the generally high values of SR found in herbivores throughout Norway (figure 1), except from the coastal areas. Additionally, when excluding the coastal areas, both mammals and birds are widely distributed across Norway, which means that they are likely to co-occur within most areas across Norway. Hence, cells where they both occur, will naturally represent a higher span of the phylogeny, and thus higher PD.

In addition, previous studies on patterns of PD in mammals and birds have shown that they tend to have different environmental drivers of clustering and overdispersion (Voskamp et al., 2017; Zupan et al., 2014), which could cause spatial mismatches when comparing values of mammals and birds combined as herbivores against pattern of PD in producers. Furthermore, this study excluded herbivorous livestock species in Norway, such as cattle (*Bos taurus*), domestic sheep (*Ovis aries*) and goat (*Capra aegagrus hircus*). The livestock species, though recently declining in their abundance in unenclosed land within Norway (Speed, Austrheim, Kolstad, & Solberg, 2019), is well distributed throughout Norway and would add to the species richness of herbivores in general. Similarly, the range maps of reindeer (*Rangifer tarandus*) from IUCN seem to only cover ranges known to wild reindeer (Norsk villreinsenter, n.d.), meaning that inclusion of the semi-domesticated reindeer would add to herbivore SR, especially in mid- and northern Norway, where pastures for semi-domesticated reindeer are found. Overall, inclusion of abovementioned species into the study, could have affect the relationship between plant and herbivore PD, through its direct effect on herbivore SR.

It should also be mentioned that the distribution data for the producers is retrieved from GBIF, which is based on observations, and hence absence of data does not necessarily mean that no plant species are present. This could further have impacted the relationship between producer's PD and the other trophic groups' PD in general.

Associations between primary consumers and higher trophic levels

Strong correlations in the spatial pattern of phylodiversity (PD) was found between herbivores and carnivores (r = 0.92), invertivores (r = 0.9) and omnivores (r = 0.95) (figure 3), as hypothesized (H_1). Despite high correlations, herbivores deviate to some degree in the spatial pattern of PD (figure 2b) compared to the patterns of PD observed for the secondary consumers (i.e. carnivores, invertivores and omnivores) (figure 2d-f). For example, herbivores do not have the relatively low PD in the mountainous areas in south-western Norway. Instead the herbivores have generally high values of PD throughout all of Norway, even in the northernmost areas. Additionally, the herbivores have some patches of relatively high values of PD in south central Norway.

Safi et al. (2011) found strong correlations between prey (i.e. primary consumers) and predator (i.e. secondary consumers) SR. Nevertheless, the effects of prey SR on predator SR were stronger than the other way around; prey SR were stronger associated to climate and productivity than predator SR. Following this, it is reasonable that the observed pattern of PD within herbivores differs from the patterns of the secondary consumers, due to the fact that they vary in which environmental variables are their most important drivers of SR, which could affect the distributional pattern of PD as well. Then again, looking at spatial distribution of SR between herbivores and the secondary consumers (figure 1), they seem to resemble each other more closely, compared to the patterns of PD. This higher resemblance between herbivores and secondary consumers in SR is further supported by the slightly higher correlations found between herbivores SR and SR of the secondary consumers (figure A1, appendix A). This implies that some other variable than SR is affecting the deviations in the spatial pattern of PD between herbivores and secondary consumers than SR itself.

Moreover, strong correlations were found within the secondary consumers as well. Carnivores, invertivores and omnivores had correlations of 0.95 and 0.96 (figure 4). These strong correlations were mirrored in the maps that represented spatial distributions of PD within the respective trophic groups (figure 1 d-f). Visually interpreting the maps, the areas of relatively

high or low values of PD tend to coincide across the respective groups, especially between carnivores and omnivores. A possible explanation to this could be that carnivores and omnivores are more similar in terms of species composition, i.e. which taxa is included and the rations between the taxa compared to invertivores (table 1). For example, the invertivores have higher ratio of birds, and is the only group to include all taxa. Given that prior studies have shown that the spatial distribution of PD differ between taxa (Fritz & Rahbek, 2012; Voskamp et al., 2017), it is reasonable to think that the invertivores have some discrepancies in the spatial pattern of PD compared to the other two due to its inclusion of more taxa.

It was hypothesized that areas with high phylogenetic diversity in plants, would have correspodning high phylogenetic diversity in invertivores, which in this study consist of mainly inseact eaters (H_3). The observed relationship between plant PD and invertivore PD have a correlation of 0.52, which indicates a moderate, positive association between the two. Furthermore, from visually inspecting the residuals from the regression of PD in invertivores against plant PD (figure 5c), it is apparent that there are several areas where invertivore PD is not well explained by plant PD (i.e. high absolute values of residuals). Regions with high absolute value of residuals are mainly located along the coastline of Norway. The plants had in general higher values of PD along the coastal areas, compared to the remaning trophic groups, including invertivores. Additionally, invertivores tended to have higher values of PD relative to plants in the remaning parts of the country. This further illustrates the deviations in the relationship in PD between plants and invertivores. Additionally, the coast areas—at least in the southern part of the country—were locations for phylogenetic overdipsersion in plants, which could further lead to deviations in their relationship.

4.3 Spatial patterns of phylogenetic clustering and overdispersion

Different environmental variables combines with trophic interactions to affect the distribution of PD within different taxa (Safi et al., 2011; Voskamp et al., 2017). And prior studies of phylogenetic diversity within a single trophic level have shown how integration of climatic variables into study of patterns of phylogenetic clustering and overdispersion can explain some of the patterns of phylogenetic clustering and overdispersion.

The observed number of areas with significantly different values of PD (either overdispersion or clustering), varied considerably between the different trophic groups. The producers (figure

A3) have the highest number of significant areas, both positive and negative, followed by invertivores. These two trophic group have higher SR relative to the others, with 1 118 and 132 species, respectively. These observations suggest that there may be a link between the number of species within respective groups, and the number of significant areas. This assumption is further supported by herbivores having both the lowest number of significant areas, and the lowest number of species (25). However, the pattern is interrupted when looking at carnivores and omnivores. Carnivores have a higher number of species (44) than omnivores (64), but carnivores have more significant areas than omnivores, though these are only significantly low values, unlike omnivores that have both high and low. Taken together, these results suggest that the results from the randomization test should be interpreted with care, as the number of significant areas seem to be related to the number of species within the respective trophic groups. Hence, few significant areas can be a matter of statistical power, and might not reflect a genuine pattern of phylogenetic clustering and overdispersion.

As mentioned, both herbivores (figure 6a) and omnivores (figure 6d) have relatively few significant areas, which makes it difficult to discuss possible climatic conditions that could underpin their distribution of phylogenetic clustering and dispersion. Carnivores (figure 6b) have areas of phylogenetic clustering throughout northern Norway, as well as at the west coast and some areas within the central parts of southern Norway. The west coast is characterized by high values of annual precipitation, while the northern areas have relative low values of precipitation (figure A4, appendix A). In addition, the temperatures tend to be higher at the west coast compared to the central and northern Norway. Given that phylogenetic clustering within carnivores is found in areas with contradictory climate conditions, these results make it difficult to assess potential climatic conditions that affect the distribution of clustering in carnivores. The invertivores have areas of both phylogenetic distribution and clustering, that seem to follow some of the same patterns as found for producers (figure A3, appendix A) with phylogenetic overdispersion located along the south coast, and phylogenetic clustering in central Norway and in the mi- and northern Norway. This could imply that either patterns of PD in plants and invertivores are driven by some of the same climatic variables, or it could further support the hypothesis (H_3) that PD in plants are associated with PD in invertivores.

Deviations in associations

Herbivores, omnivores and invertivores have a substantial amount of variation in PD that is not explained by the PD in plants (figure 5 a-c), which is in contradiction from what expected (H_1)

This is perhaps not surprising, given the generally low correlations found between PD in producers and invertivores, herbivores and omnivores (varying from 0.34 to 0.52). All the trophic groups had similar patterns in their distribution of areas with high deviations in PD according to plant PD (i.e. residuals). High absolute values of residuals were found primarily along the coast and border to Sweden. As mentioned, the coastal areas generally have low SR for the different taxa except for producers (figure A2), meaning that the residuals in these areas could be caused by low species coverage of animals compared to producers in these areas. Moreover, the coast areas consist of many small islands, resulting in raster cells here containing a significant amount of water compared to land areas, which again can give a wrongful interpretation of the relationships between plant PD and the investigated groups' PD. In the northern areas for herbivore PD regressed against plant PD, coincide well with cells excluded from the study of Ida M Mienna et al. (2020) due to low completeness in plant species.

Oppositely, for carnivores, invertivores and omnivores, much of their variation in PD can be explained by variation in herbivore PD (figure 5d-f), illustrated by the low absolute values of the residuals found from the linear relationship between these trophic groups and plant PD. Again, this is not surprising giving the relatively good correlations found between the respective trophic groups. Although, there are still tendencies to some deviations in their relationships along the coast of mid-Norway, and in and around the Oslofjord, indicating that in these areas, other variables than herbivore PD contribute to the respective groups PD.

4.4 Limitations and further implications

This study has several potential areas of improvement. For example, the choice of method to assess areas with phylogenetic clustering and overdispersion did not give the results as expected, probably due to low number of species within each group, and hence low sample sizes and statistical power. An alternative way to assess areas of phylogenetic clustering and overdispersion, is to regress PD against SR (Swenson, 2014). This would perhaps give a truer picture of the spatial distribution of phylogenetically clustering and overdispersion within each of the trophic groups.

Furthermore, the removal of cells that contains a substantially amount of water along the coast, would potentially give a more correct illustration of the associations between plant and animal PD in these areas. Also, the fact that both an ultrametric phylogeny and a non-ultrametric

phylogeny were used, could affect the relationships between plant and animal PD. Lastly, the categorizing of animals into trophic groups were based on certain criteria. If those were changed, e.g. granivores were not sorted out as a separate group, perhaps the associations in PD would be different.

To better understand the relative role of trophic interactions in driving and regulating the phylogenetic structures of communities in Norway, future research should include environmental variables as a possible structuring and driving factors of phylogenetic diversity as well.

5. Conclusion

This study set out to assess the degree of associations in PD between different trophic levels throughout Norway. Positive, significant associations in PD were found between all trophic groups included in this study. However, the degree of associations varied, indicating that trophic interactions is not the only driver of the phylogenetic structure of communities in Norway. Also, mapping the residuals from regression analyses showed how PD covaried and differed in space between the trophic groups.

The degree of correlation between producers and higher trophic levels were relatively low, which were argued to have several different explanations. Furthermore, the study found a strong, positive correlation between spatial patterns of SR and PD throughout Norway, which is in accordance with results from similar studies.

6. Referances

Alsos, I. G., Eidesen, P. B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G. H., . . . Brochmann, C. (2007). Frequent long-distance plant colonization in the changing Arctic. *Science, 316*(5831), 1606-1609.

Bailey, J. K., Wooley, S. C., Lindroth, R. L., & Whitham, T. G. (2006). Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology letters, 9*(1), 78-85.

Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: from individuals to ecosystems*. New Jersey: Blackwell publishing

Bivand, R. S., & Pebesma, E. J. (2005). Classes and methods for spatial data in R. *R News, 5* (2). Retrieved from https://cran.r-project.org/doc/Rnews/

Brodersen, J., Post, D. M., & Seehausen, O. (2018). Upward Adaptive Radiation Cascades: Predator Diversification Induced by Prey Diversification. *Trends Ecol Evol, 33*(1), 59-70.

Cadotte, M. W., & Davies, T. J. (2016). *Phylogenies in Ecology: A Guide to Concepts and Methods*: New Jersey: Princeton University Press.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science advances, 1*(5), e1400253.

Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., . . . McCabe, A. M. (2009). The last glacial maximum. *Science, 325*(5941), 710-714.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., . . . O'Brien, E. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters, 7*(12), 1121-1134.

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, Or, The Preservation of Favoured Races in the Struggle for Life*. London: J. Murray.

Davies, T. J., & Buckley, L. B. (2011). Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1576), 2414-2425.

Dolmen, D. (2008). *Norske amfibier og reptiler (Feltherpetologisk guide)–Bli med ut!* 9: 1-78. Trondheim: Tapir akademisk forlag.

Elton, C. (1946). Competition and the structure of ecological communities. *The Journal of Animal Ecology*, 54-68.

Emerson, B. C., & Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in ecology & evolution, 23*(11), 619-630.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological conservation, 61*(1), 1-10.

Fergnani, P. N., & Ruggiero, A. (2017). The latitudinal diversity gradient in South American mammals revisited using a regional analysis approach: The importance of climate at extra-tropical latitudes and history towards the tropics. *PLoS One, 12*(9).

Fog, K., de Lasson, D. R., & Schmedes, A. (1997). *Nordens padder og krybdyr*. København: Gad forlag.

Fritz, S. A., & Rahbek, C. (2012). Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography, 39*(8), 1373-1382.

Henriksen, S., & Hilmo, O. (2015). Norsk rødliste for arter 2015. *Artsdatabanken, Norge, 6*.

Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological journal of the Linnean Society, 68*(1-2), 87-112.

Hijmans, R. J. (2019). raster: Geographic Data Analysis and Modelling (Version 3.0-7). Retrieved from https://CRAN.R-project.org/package=raster

Johnson, M. T., & Agrawal, A. A. (2005). Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (Oenothera biennis). *Ecology, 86*(4), 874-885.

Johnson, M. T., & Stinchcombe, J. R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends in ecology & evolution, 22*(5), 250-257.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., . . . Webb, C. O. (2010). Picante: R tools for integrating phylogenis and ecology. *Bioinformatics, 26*, 1463-1464.

Kembel, S. W., Cowan, P. D., Helmuus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S.P., Webb, C.O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics, 26*, 1463-1464.

Kling, M. M., Mishler, B. D., Thornhill, A. H., Baldwin, B. G., & Ackerly, D. D. (2019). Facets of phylodiversity: evolutionary diversification, divergence and survival as conservation targets. *Philosophical Transactions of the Royal Society B, 374*(1763), 20170397.

Kumar, S., Stecher, G., Suleski, M., & Hedges, S. B. (2017). TimeTree: A Resource for Timelines, Timetrees, and Divergence Times. *Molecular Biology and Evolution, 34*(7), 1812-1819.

MacArthur, R. H. (1965). Patterns of species diversity. *Biological reviews, 40*(4), 510-533.

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology letters, 13*(9), 1085-1093.

Mienna, I. M. (2018). *Patterns and Drivers of Phylogenetic Diversity and Endemism in the Norwegian Vascular Flora.* (Master thesis, NTNU). Trondheim.

Mienna, I. M., Speed, J. D., Bendiksby, M., Thornhill, A. H., Mishler, B. D., & Martin, M. D. (2020). Differential patterns of floristic phylogenetic diversity across a post-glacial landscape. *Journal of Biogeography, 47*(4), 915-926.

Mishler, B. D., Knerr, N., González-Orozco, C. E., Thornhill, A. H., Laffan, S. W., & Miller, J. T. (2014). Phylogenetic measures of biodiversity and neo-and paleo-endemism in Australian Acacia. *Nature Communications, 5*, 4473.

Norsk villreinsenter. (n.d.). Villreinområdene. Retrieved from villrein.no/om-villreinomrdene

Pavoine, S., & Bonsall, M. B. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biological reviews, 86*(4), 792-812.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography, 12*(5), 361-371.

Primack, R. B. (2014). *Essentials of Conservation Biology.* Massachusetts: Sinauer.

R Core Team. (2019). R: A language and environment for statistical computing (version 3.6.2). Vienna, Austria: Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Renner, S. (2004). Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences, 165*(S4), S23-S33.

Ross, N. (2020). fasterize: Fast Polygon to Raster Conversion. (Version 1.0.2). Retrieved from https://CRAN.R-project.org/package=fasterize

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos Trans R Soc Lond B Biol Sci, 366*(1577), 2536-2544.

Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W. D., Lenoir, J., Sandel, B., . . . Svenning, J.-C. (2013). Mammal predator and prey species richness are strongly linked at macroscales. *Ecology, 94*(5), 1112-1122.

Schweiger, O., Klotz, S., Durka, W., & Kühn, I. (2008). A comparative test of phylogenetic diversity indices. *Oecologia, 157*(3), 485-495.

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.-A., . . . Gonçalves, J. (2014). Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia, 35*(1), 1-31.

Skjelbred, I. Å. (2017). *Phylogenetic Diversity of Arctic Vertebrate Herbivores.* (Master thesis, NTNU). Trondheim.

Speed, J. D., Austrheim, G., Kolstad, A. L., & Solberg, E. J. (2019). Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. *PLoS One, 14*(5).

Speed, J. D. M., Skjelbred, I. Å., Barrio, I. C., Martin, M. D., Berteaux, D., Bueno, C. G., . . . Soininen, E. M. (2019). Trophic interactions and abiotic factors drive functional and phylogenetic structure of vertebrate herbivore communities across the Arctic tundra biome. *Ecography, 42*(6), 1152-1163.

Swenson, N. G. (2011). The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany, 98*(3), 472-480.

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R.* New York: Springer.

Voskamp, A., Baker, D. J., Stephens, P. A., Valdes, P. J., & Willis, S. G. (2017). Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of Biogeography, 44*(4), 709-721.

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences, 105*(Supplement 1), 11466-11473.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual review of ecology and systematics, 33*(1), 475-505.

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in ecology & evolution, 19*(12), 639-644.

Wiens, J. J., Pyron, R. A., & Moen, D. S. (2011). Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology letters, 14*(7), 643-652.

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology, 95*(7), 2027-2027.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., . . . Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol Rev Camb Philos Soc, 88*(1), 15-30.

Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., . . . Thuiller, W. (2014). Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Diversity and Distributions, 20*(6), 674-685.

APPENDIX A

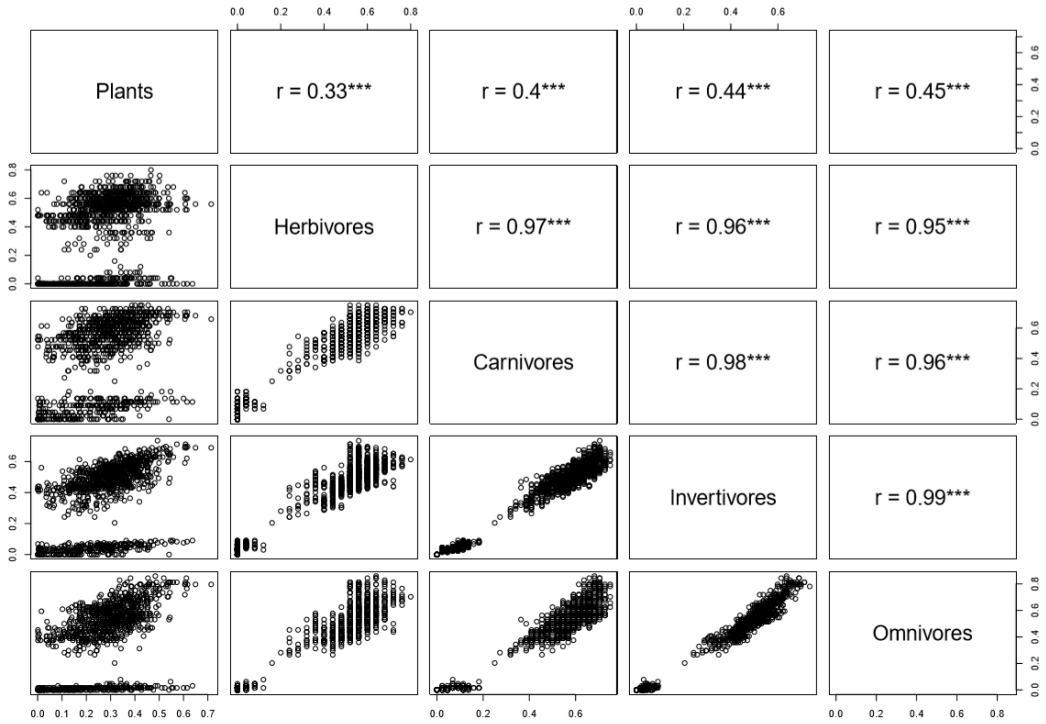

Figure A1. Results from correlation analysis of species richness (SR) between given trophic levels. The resulting correlation coefficient (r) between each of the trophic groups, is shown together with an asterisk that indicate the level of significance (*** = $p < 0.001$).

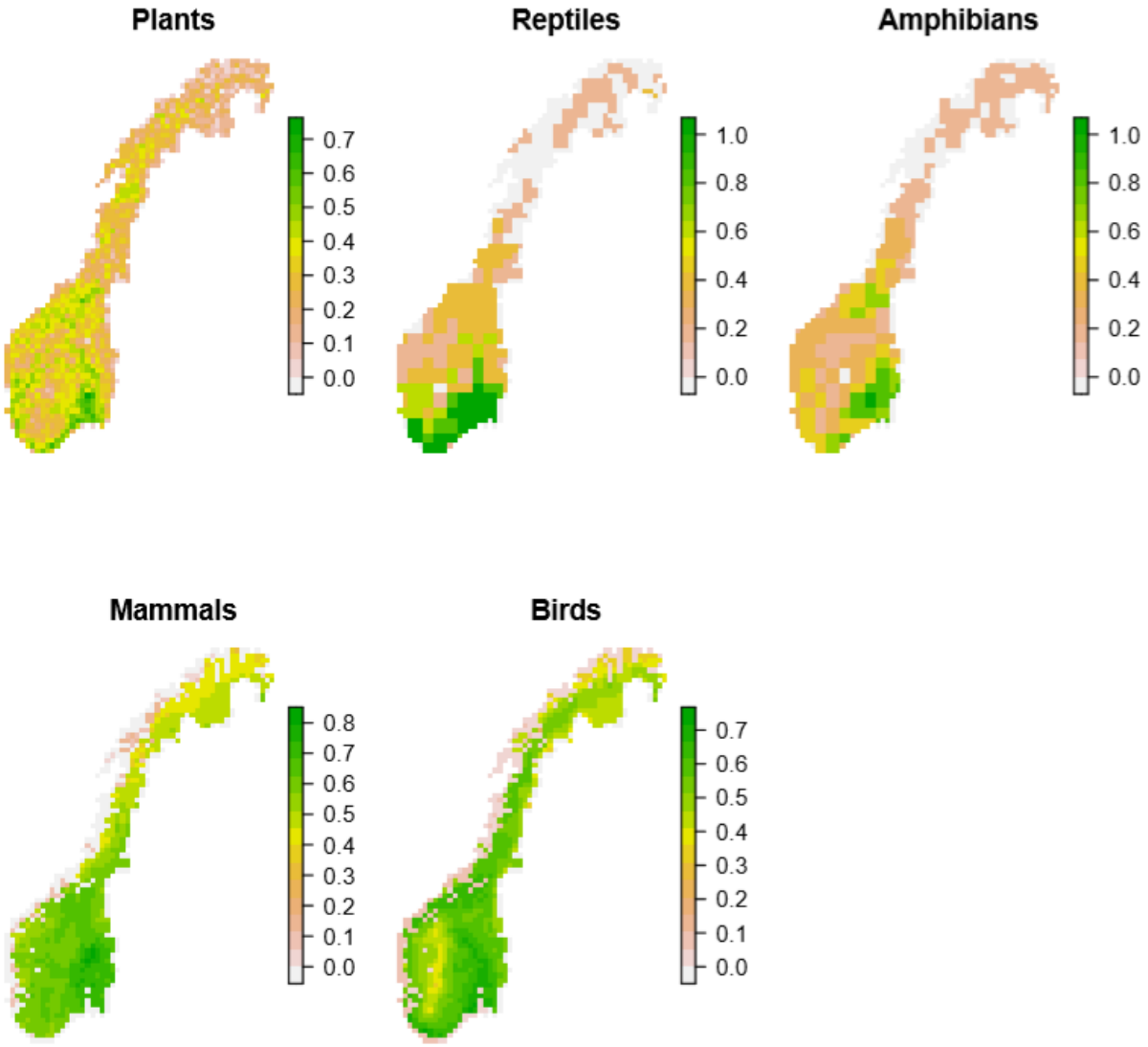

Figure A2. Distribution maps of species richness (SR) for included taxonomic groups (plants, amphibians, reptiles, mammals, and birds). All maps projected to WGS 84 / UTM zone 33N.

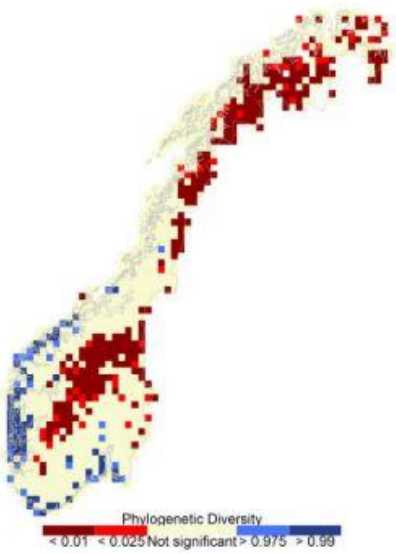

Figure A3. Results of spatial randomizations of PD in vascular plants. From (Ida Marielle Mienna, 2018). WGS 84 / UTM zone 33N.

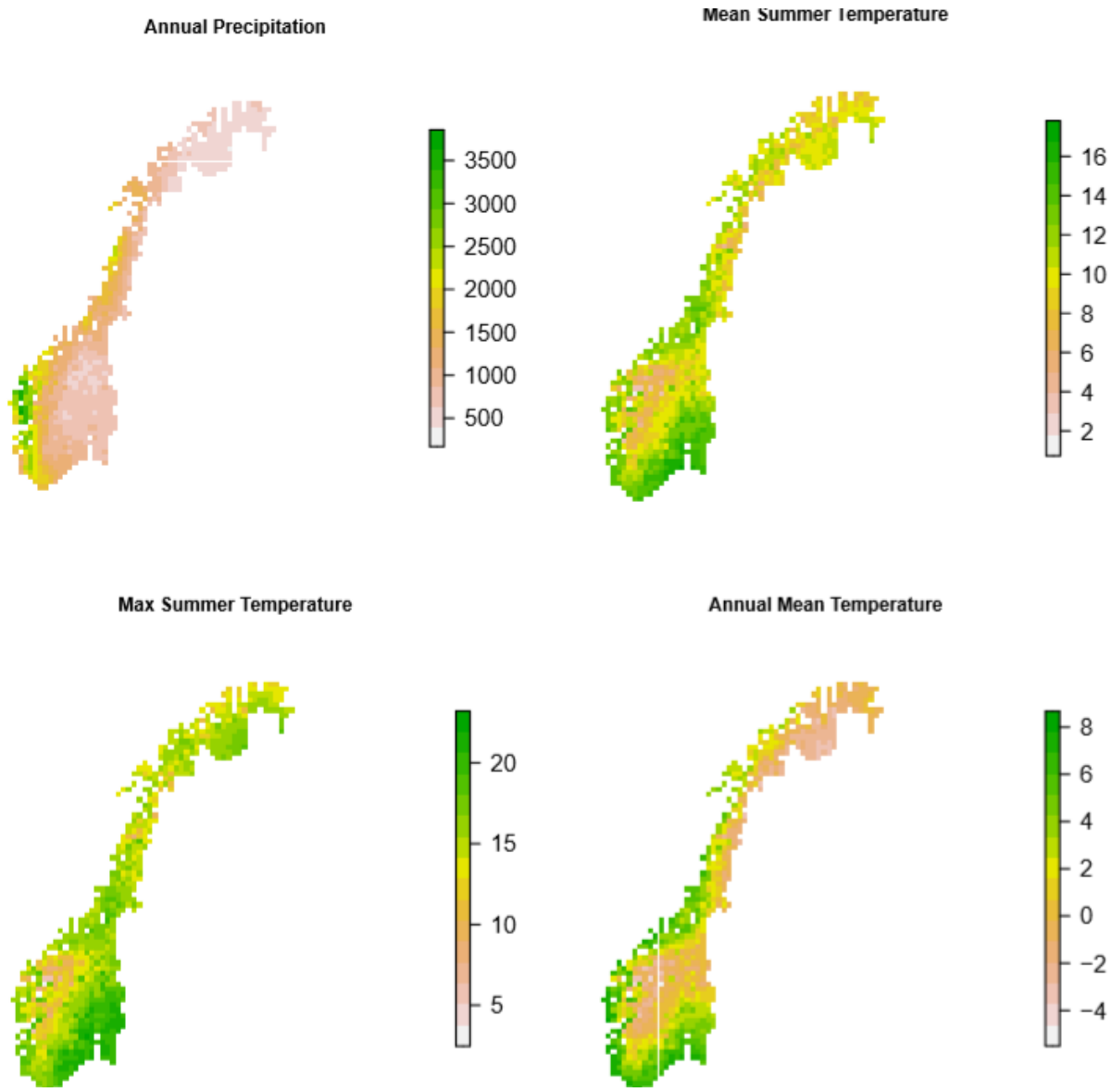

Figure A4. Climatic variables from WorldClim (Hijmans, 2019). All variables are in 20x20- km grid cells and projected to WGS 84 / UTM zone 32N.

Tabell A1. Examined species (269) organized into taxonomic and trophic group.

Trophic group	Scientific species name	Taxonomic group
carnivore	Lynx lynx	mammal
carnivore	Vulpes vulpes	mammal
carnivore	Vulpes lagopus	mammal
carnivore	Canis lupus	mammal
carnivore	Mustela erminea	mammal
carnivore	Mustela putorius	mammal
carnivore	Mustela nivalis	mammal
carnivore	Martes martes	mammal
carnivore	Mergus serrator	bird
carnivore	Mergus merganser	bird
carnivore	Bubo bubo	bird
carnivore	Bubo scandiaca	bird
carnivore	Strix aluco	bird
carnivore	Strix uralensis	bird
carnivore	Surnia ulula	bird
carnivore	Glaucidium passerinum	bird
carnivore	Aegolius funereus	bird
carnivore	Asio otus	bird
carnivore	Asio flammeus	bird
carnivore	Stercorarius longicaudus	bird
carnivore	Sterna hirundo	bird
carnivore	Sterna paradisaea	bird
carnivore	Pandion haliaetus	bird
carnivore	Circus cyaneus	bird
carnivore	Accipiter nisus	bird
carnivore	Accipiter gentilis	bird
carnivore	Buteo buteo	bird
carnivore	Buteo lagopus	bird
carnivore	Aquila chrysaetos	bird
carnivore	Falco tinnunculus	bird
carnivore	Falco columbarius	bird
carnivore	Falco rusticolus	bird
carnivore	Falco peregrinus	bird
carnivore	Podiceps cristatus	bird
carnivore	Podiceps auritus	bird
carnivore	Phalacrocorax carbo	bird
carnivore	Ardea cinerea	bird
carnivore	Gavia stellata	bird
carnivore	Gavia arctica	bird
carnivore	Gavia adamsii	bird
carnivore	Lanius excubitor	bird
carnivore	Coronella austriaca	reptile
carnivore	Natrix natrix	reptile

carnivore	Vipera berus	reptile
granivore	Coturnix	bird
granivore	Carduelis chloris	bird
granivore	Emberiza pusilla	bird
granivore	Emberiza rustica	bird
herbivore	Castor fiber	mammal
herbivore	Microtus agrestis	mammal
herbivore	Microtus oeconomus	mammal
herbivore	Arvicola amphibius	mammal
herbivore	Lemmus lemmus	mammal
herbivore	Myopus schisticolor	mammal
herbivore	Lepus timidus	mammal
herbivore	Alces alces	mammal
herbivore	Capreolus capreolus	mammal
herbivore	Rangifer tarandus	mammal
herbivore	Cervus elaphus	mammal
herbivore	Lagopus lagopus	bird
herbivore	Lagopus muta	bird
herbivore	Tetrao tetrix	bird
herbivore	Tetrao urogallus	bird
herbivore	Bonasa bonasia	bird
herbivore	Cygnus olor	bird
herbivore	Cygnus cygnus	bird
herbivore	Anser fabalis	bird
herbivore	Anser erythropus	bird
herbivore	Anser anser	bird
herbivore	Branta leucopsis	bird
herbivore	Anas strepera	bird
herbivore	Anas penelope	bird
herbivore	Plectrophenax nivalis	bird
invertivore	Erinaceus europaeus	mammal
invertivore	Sorex caecutiens	mammal
invertivore	Sorex minutus	mammal
invertivore	Sorex araneus	mammal
invertivore	Sorex minutissimus	mammal
invertivore	Eptesicus nilssonii	mammal
invertivore	Pipistrellus nathusii	mammal
invertivore	Pipistrellus pygmaeus	mammal
invertivore	Nyctalus noctula	mammal
invertivore	Barbastella barbastellus	mammal
invertivore	Plecotus auritus	mammal
invertivore	Vespertilio murinus	mammal
invertivore	Myotis nattereri	mammal
invertivore	Myotis mystacinus	mammal
invertivore	Myotis brandtii	mammal
invertivore	Myotis daubentonii	mammal

invertivore	Tadorna tadorna	bird
invertivore	Anas clypeata	bird
invertivore	Aythya fuligula	bird
invertivore	Aythya marila	bird
invertivore	Somateria mollissima	bird
invertivore	Polysticta stelleri	bird
invertivore	Clangula hyemalis	bird
invertivore	Melanitta nigra	bird
invertivore	Melanitta fusca	bird
invertivore	Bucephala clangula	bird
invertivore	Mergellus albellus	bird
invertivore	Jynx torquilla	bird
invertivore	Dendrocopos minor	bird
invertivore	Dendrocopos leucotos	bird
invertivore	Dendrocopos major	bird
invertivore	Picoides tridactylus	bird
invertivore	Dryocopus martius	bird
invertivore	Picus viridis	bird
invertivore	Picus canus	bird
invertivore	Cuculus canorus	bird
invertivore	Apus apus	bird
invertivore	Caprimulgus europaeus	bird
invertivore	Scolopax rusticola	bird
invertivore	Gallinago media	bird
invertivore	Gallinago gallinago	bird
invertivore	Lymnocryptes minimus	bird
invertivore	Limosa limosa	bird
invertivore	Limosa lapponica	bird
invertivore	Numenius phaeopus	bird
invertivore	Tringa erythropus	bird
invertivore	Tringa totanus	bird
invertivore	Tringa nebularia	bird
invertivore	Tringa ochropus	bird
invertivore	Tringa glareola	bird
invertivore	Actitis hypoleucos	bird
invertivore	Arenaria interpres	bird
invertivore	Calidris minuta	bird
invertivore	Calidris temminckii	bird
invertivore	Calidris maritima	bird
invertivore	Calidris alpina	bird
invertivore	Limicola falcinellus	bird
invertivore	Philomachus pugnax	bird
invertivore	Phalaropus lobatus	bird
invertivore	Haematopus ostralegus	bird
invertivore	Pluvialis apricaria	bird
invertivore	Charadrius hiaticula	bird

invertivore	Charadrius dubius	bird
invertivore	Eudromias morinellus	bird
invertivore	Vanellus vanellus	bird
invertivore	Larus ridibundus	bird
invertivore	Larus minutus	bird
invertivore	Pernis apivorus	bird
invertivore	Falco subbuteo	bird
invertivore	Tachybaptus ruficollis	bird
invertivore	Lanius collurio	bird
invertivore	Cinclus cinclus	bird
invertivore	Turdus merula	bird
invertivore	Turdus pilaris	bird
invertivore	Muscicapa striata	bird
invertivore	Ficedula hypoleuca	bird
invertivore	Luscinia luscinia	bird
invertivore	Luscinia svecica	bird
invertivore	Phoenicurus ochruros	bird
invertivore	Phoenicurus phoenicurus	bird
invertivore	Saxicola rubetra	bird
invertivore	Saxicola torquatus	bird
invertivore	Oenanthe oenanthe	bird
invertivore	Sitta europaea	bird
invertivore	Certhia familiaris	bird
invertivore	Troglodytes troglodytes	bird
invertivore	Parus palustris	bird
invertivore	Parus montanus	bird
invertivore	Parus cinctus	bird
invertivore	Parus cristatus	bird
invertivore	Parus caeruleus	bird
invertivore	Aegithalos caudatus	bird
invertivore	Riparia riparia	bird
invertivore	Hirundo rustica	bird
invertivore	Delichon urbicum	bird
invertivore	Regulus regulus	bird
invertivore	Locustella naevia	bird
invertivore	Acrocephalus schoenobaenus	bird
invertivore	Acrocephalus scirpaceus	bird
invertivore	Acrocephalus palustris	bird
invertivore	Hippolais icterina	bird
invertivore	Phylloscopus trochilus	bird
invertivore	Phylloscopus collybita	bird
invertivore	Phylloscopus sibilatrix	bird
invertivore	Phylloscopus borealis	bird
invertivore	Panurus biarmicus	bird
invertivore	Sylvia atricapilla	bird
invertivore	Sylvia borin	bird

invertivore	Sylvia communis	bird
invertivore	Sylvia curruca	bird
invertivore	Sylvia nisoria	bird
invertivore	Lullula arborea	bird
invertivore	Eremophila alpestris	bird
invertivore	Motacilla alba	bird
invertivore	Motacilla flava	bird
invertivore	Motacilla cinerea	bird
invertivore	Anthus trivialis	bird
invertivore	Anthus pratensis	bird
invertivore	Anthus cervinus	bird
invertivore	Anthus petrosus	bird
invertivore	Prunella modularis	bird
invertivore	Fringilla coelebs	bird
invertivore	Emberiza hortulana	bird
invertivore	Calcarius lapponicus	bird
invertivore	Bufo bufo	amphibian
invertivore	Pelophylax lessonae	amphibian
invertivore	Rana arvalis	amphibian
invertivore	Rana temporaria	amphibian
invertivore	Lissotriton vulgaris	amphibian
invertivore	Triturus cristatus	amphibian
invertivore	Anguis fragilis	reptile
invertivore	Zootoca vivipara	reptile
omnivore	Sciurus vulgaris	mammal
omnivore	Sicista betulina	mammal
omnivore	Myodes rutilus	mammal
omnivore	Myodes rufocanus	mammal
omnivore	Myodes glareolus	mammal
omnivore	Apodemus flavicollis	mammal
omnivore	Apodemus sylvaticus	mammal
omnivore	Mus musculus	mammal
omnivore	Rattus norvegicus	mammal
omnivore	Neomys fodiens	mammal
omnivore	Gulo gulo	mammal
omnivore	Meles meles	mammal
omnivore	Lutra lutra	mammal
omnivore	Ursus arctos	mammal
omnivore	Anas platyrhynchos	bird
omnivore	Anas acuta	bird
omnivore	Anas querquedula	bird
omnivore	Anas crecca	bird
omnivore	Columba oenas	bird
omnivore	Columba palumbus	bird
omnivore	Streptopelia decaocto	bird
omnivore	Grus grus	bird

omnivore	Rallus aquaticus	bird
omnivore	Crex crex	bird
omnivore	Porzana porzana	bird
omnivore	Gallinula chloropus	bird
omnivore	Fulica atra	bird
omnivore	Numenius arquata	bird
omnivore	Stercorarius parasiticus	bird
omnivore	Larus fuscus	bird
omnivore	Haliaeetus albicilla	bird
omnivore	Garrulus glandarius	bird
omnivore	Perisoreus infaustus	bird
omnivore	Pica pica	bird
omnivore	Nucifraga caryocatactes	bird
omnivore	Corvus monedula	bird
omnivore	Corvus frugilegus	bird
omnivore	Corvus corax	bird
omnivore	Bombycilla garrulus	bird
omnivore	Turdus torquatus	bird
omnivore	Turdus iliacus	bird
omnivore	Turdus philomelos	bird
omnivore	Turdus viscivorus	bird
omnivore	Erithacus rubecula	bird
omnivore	Sturnus vulgaris	bird
omnivore	Parus ater	bird
omnivore	Parus major	bird
omnivore	Alauda arvensis	bird
omnivore	Passer domesticus	bird
omnivore	Passer montanus	bird
omnivore	Fringilla montifringilla	bird
omnivore	Carduelis spinus	bird
omnivore	Carduelis carduelis	bird
omnivore	Carduelis flammea	bird
omnivore	Carduelis flavirostris	bird
omnivore	Carduelis cannabina	bird
omnivore	Carpodacus erythrinus	bird
omnivore	Pinicola enucleator	bird
omnivore	Loxia pytyopsittacus	bird
omnivore	Loxia curvirostra	bird
omnivore	Pyrrhula pyrrhula	bird
omnivore	Coccothraustes coccothraustes	bird
omnivore	Emberiza citrinella	bird
omnivore	Emberiza schoeniclus	bird