



Assessing the relation between geodiversity and species richness in mountain heaths and tundra landscapes

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Received: 3 March 2023 / Accepted: 4 June 2023
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Abstract

Context Recent studies show that geodiversity—the diversity of Earth’s landforms, materials, and processes—has a positive relationship with biodiversity at a landscape scale. However, there is a substantial lack of evidence from finer scales, although this knowledge could improve the understanding of biodiversity patterns.

Objectives We investigate whether plot-scale geodiversity and plant species richness (vascular plants,

bryophytes, lichens, and total richness) are positively linked in different tundra landscapes.

Methods We collected geodiversity (presence of different geofeatures) and plant species richness data from 165 sites in three distinct regions: isolated low-lying mountain heaths, and in sporadic and continuous mountain heaths and tundra. We used non-metric multidimensional scaling (NMDS) ordination to explore the correlations between the composition of geofeatures and species richness, followed by univariate and multivariate generalized linear models (GLM), to assess whether georichness is important for species richness.

Results Geofeature composition was linked to species richness in all regions, as indicated by NMDS ordination. Both univariate and multivariate GLM models showed statistically significant relationship between species richness and georichness in all studied species richness groups in continuous Arctic-alpine tundra. Additionally, there was a positive link between georichness and lichen richness in isolated boreal mountain tops.

Main conclusion We showed that plot-scale geodiversity has a positive relationship with species richness, yet the effect varies regionally and between species groups. Our study provides strong empirical evidence that geodiversity supports species richness in continuous Arctic-alpine tundra. This information can be used in species richness models but also be applied in biodiversity management and conservation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-023-01702-1>.

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Keywords Biodiversity · Geodiversity · Georichness · Mountain heaths · Species richness · Tundra

Introduction

The importance of gaining information on local and landscape scale biodiversity patterns, which align closely with conservation investment and action (IPBES 2019; Wyborn and Evans 2021), is brought forth in current ecological discussion (Pärtel et al. 2016). A wide variety of factors affect species richness at finer scales and many of them are context dependent (Whittaker et al. 2001; Catford et al. 2022). One potential but largely unexplored driver of plot-scale biodiversity is geodiversity. Geodiversity considers holistically the abiotic conditions (bedrock, soil, hydrology, and geomorphology) of the Earth's surface and sub-surface (Gray 2013). Therefore, it is a combination of different geodiversity elements, or geofeatures (such as rock types, soil types or landforms) at a site (Serrano and Ruiz-Flaño 2007; Hjort et al. 2022). Geodiversity is often measured quantitatively, for example with different indices and richness measures (Boothroyd and McHenry 2019), but it can also be assessed qualitatively focusing on distinct geofeatures, such as rock types, soil types or landforms (Tukiainen et al. 2019).

The positive relationship between geodiversity and biodiversity is theoretically well established (Beier et al. 2015; Antonelli et al. 2018; Knudson et al. 2018; Tukiainen et al. 2022b). It is based on the idea that diverse abiotic conditions create a stage for high species diversity by, for example, creating more niche space or supporting the existence of rare or unique biota (Stein et al. 2014; Hjort et al. 2015; Lawler et al. 2015). However, empirical evidence at finer scales is largely missing to date (Tukiainen et al. 2022b). Yet, it would increase our understanding of the abiotic drivers behind variation in species richness patterns, as well as support conservation management efforts (Crisp et al. 2022a).

Studies on the relationship between geodiversity and biodiversity have thus far focused mainly on landscape-scale at which geodiversity estimates are often based on coarse geospatial data, such as digital elevation models or geological maps (Boothroyd and McHenry 2019; Alahuhta et al. 2020; Crisp

et al. 2021). It is argued that the positive associations between geo- and biodiversity are strongest on a landscape-scale (Toivanen et al. 2019). Empirical evidence indicates that landscape-scale geodiversity is associated with vascular plant species richness (Hjort et al. 2012; Bailey et al. 2017; Toivanen et al. 2019) and number of red-listed species across several taxa (Tukiainen et al. 2017b) in high-latitude environments. Landscape-scale studies have also shown that geodiversity adds to the explanatory power of species richness models, over and above the traditionally used environmental variables, such as topography (Bailey et al. 2017; Tukiainen et al. 2017a). However, the evidence of positive geodiversity-biodiversity relationships, that is based on more detailed plot-scale data has remained scarce, although this information is increasingly needed to improve species richness modelling and to support nature conservation. Moreover, results from individual studies that use plot-scale geodiversity data, are encouraging further explorations (e.g., stream geodiversity and macroinvertebrate biodiversity, Kärnä et al. 2019; hillslope geodiversity and vascular plant biodiversity, De Falco et al. 2021; omnidiversity approach, Crisp et al. 2022b). Such approach could be especially useful in environments that are vulnerable to changing environmental conditions (Lawler et al. 2015).

In the face of rapid climate change and global biodiversity loss, it is crucial to increase the understanding of the relationships between abiotic and biotic nature in Arctic-alpine ecosystems. Although it might be challenging to fully explain the drivers and mechanisms that underlie plot-scale species richness patterns in these environments, several drivers are known to be important. For example, microtopographical variation creates an array of microclimates from cooler shades and windswept mounds to warmer depressions, leading to an increase in niche space (Kumar et al. 2006; Pajunen et al. 2008; Opedal et al. 2015). In addition to microclimate, also macroclimatic variables, such as growing degree days (GDD) or expected solar radiation, are known to be important for species richness (Bueno de Mesquita et al. 2018; Giaccone et al. 2019). Soil factors like nutrient availability and soil moisture have pronounced influence on mountain heath and tundra species richness (Kemppinen et al. 2019). For instance, locally, higher calcium concentrations create variation in pH supporting wider array of species (Gough et al. 2000; van

der Welle et al. 2003). There are also region-specific drivers that affect species richness. In Fennoscandia, for instance, especially reindeer grazing, has a pronounced influence on species richness (Kaarlejärvi et al. 2017). Recent studies from Fennoscandia also indicate that other biotic interactions, especially those related to crowberry (*Empetrum nigrum* ssp. *hermaphroditum*), may modulate species richness in the tundra (le Roux et al. 2014; Bråthen and Ravolainen 2015; Mod et al. 2016). However, the influence of geodiversity, as the diversity of abiotic features and processes (Gray 2013) on species richness alongside these drivers remains unknown, yet it could provide new insights into local species richness patterns in Arctic-alpine environments.

One reason for the missing empirical evidence of plot-scale geodiversity-biodiversity relationship has been the lack of methodologies for quantifying geodiversity at fine scales. In this study, we utilized a recently developed method to measure plot-scale geodiversity by observing different abiotic elements (i.e. geofeatures) that together form geodiversity (i.e. georichness) (Hjort et al. 2022). We applied this method to 165 study sites located at three distinct mountain heath and tundra regions in northern Fennoscandia with differences in landscape characteristics and environmental conditions: isolated low-lying mountain heaths, sporadic mountain heaths and tundra, and continuous mountain heaths and tundra. From the same study sites, we recorded the plant community composition of vascular plants, bryophytes, and lichens from 2 × 2 m vegetation plots. After describing plot-scale geodiversity in mountain heaths and tundra of Fennoscandia, we seek answers to the following questions: (1) Does certain composition of geofeatures correlate with higher species richness?, (2) Is there a positive relationship between plot-scale georichness and species richness (a) in different regions, and (b) of different species groups (total, vascular plant, bryophyte and lichen richness)?, and (3) What is the role of geodiversity in explaining species richness when other important environmental variables are considered? Following the theoretical premise (Hjort et al. 2012; Bailey et al. 2017; Toivanen et al. 2019), we expect that geodiversity is positively linked to species richness also at plot-scale with and without other environmental variables included in the analyses.

Materials and methods

Study area

The study area is located in treeless mountain heaths and tundra in northern Finland, covering latitudes from 65.80° N to 69.24° N and longitudes from 19.99° E to 29.68° E (Fig. 1; Table 1). The studied vegetation is oligotrophic and dominated by dwarf shrubs (*Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Betula nana*, *Calluna vulgaris*) with generally high abundance of bryophytes (e.g. *Dicranum* spp.) and lichens (e.g. *Cladonia* spp.). The respective habitat types are comparable to the EUNIS classification categories S1 Tundra and S2 Arctic, alpine and subalpine scrub (Chytrý et al. 2020; EUNIS terrestrial habitat classification 2021). Considering the latitudinal variation and differences in local species pools, macroclimate, elevation, and reindeer grazing pressure and regimes, we identified three distinct regions (Table 1, Online appendix S1, also in Maliniemi et al. 2018) which we studied separately. In the southernmost region, treeless mountain heath vegetation is found only on isolated low-lying boreal mountain tops (Table 1, Fig. 1). These are small in area and in the vicinity of or partly at the treeline ecotone. In region north to this treeless mountain heaths are larger in area, have longer elevational gradient and contain more tundra-like features. In this study, these are considered as sporadic mountain heaths and tundra. The northernmost region is continuous mountain heaths and tundra with a species pool that includes certain tundra species not found in other regions of this study (Online appendix S5).

Vegetation data

The total number of vegetation plots is 165 and their locations are based on a historical vegetation survey (Haapasaari 1988). All these sites have remained unaffected by direct anthropogenic land use disturbances, although few vegetation plots were located close to hiking tracks. The study plots were not spatially clustered but were scattered across different mountains and represented different exposures in all study regions. We recorded the identities and percentage covers of all species, including vascular plants, bryophytes, and lichens from 2 m x 2 m vegetation plots. The plots were placed to describe

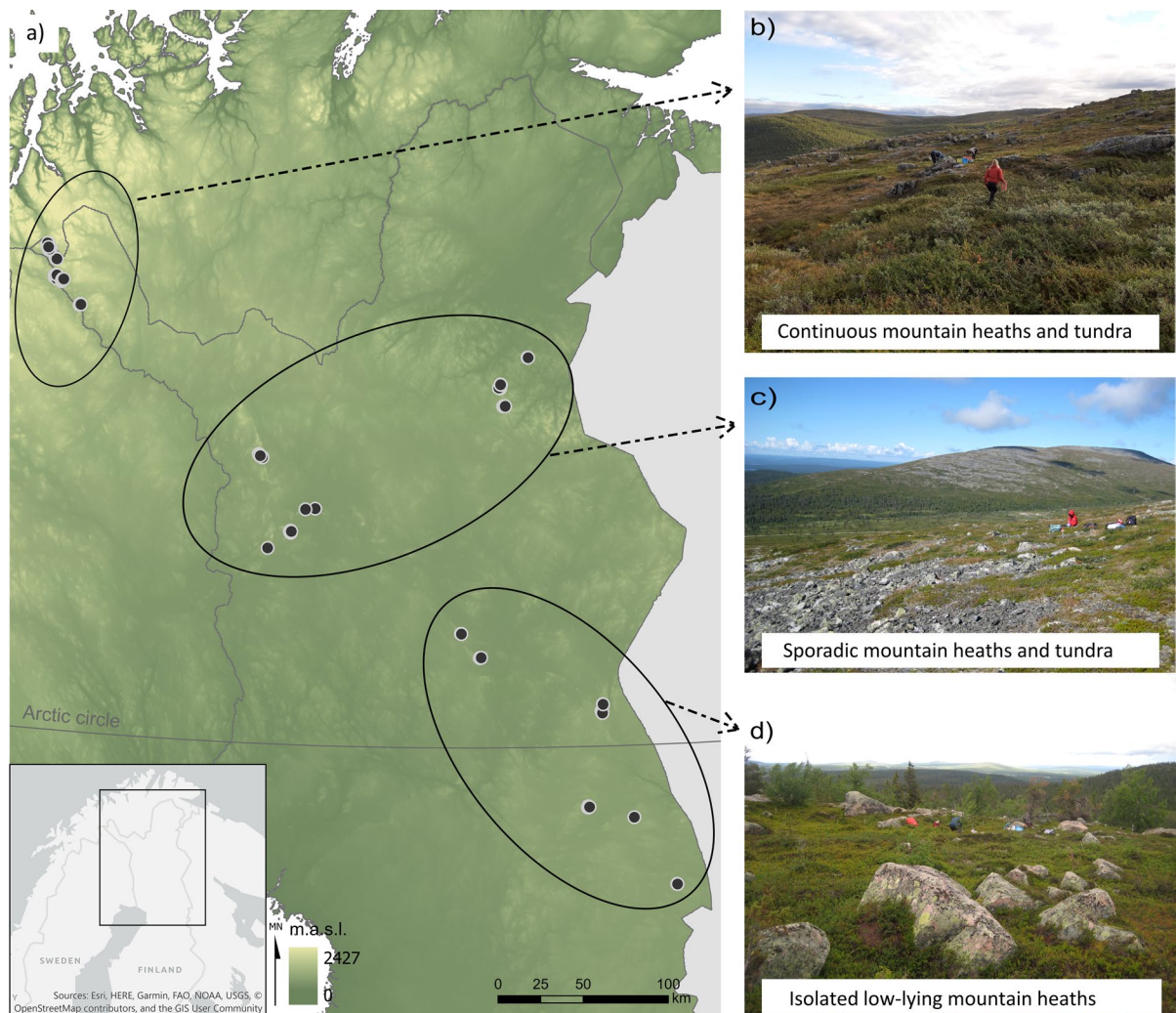


Fig. 1 **a** Location of three study regions and vegetation plots. Photographs present **b** continuous mountain heaths and tundra in the north, **c** sporadic mountain heaths and tundra and **d** isolated low-lying mountain heaths in the south

the average community composition of the dominant habitat type. Vegetation surveys were carried out during 2013–2020 by the same two surveyors. For the analysis, we treated liverworts at the genus level due to uncertainties in species level identification in the field. Otherwise, we used species-level information.

Geodiversity data

We collected data on plot-scale geodiversity in the summer 2020 from the same plot locations as the

vegetation data (Fig. 1). The geodiversity data collection is based on a field method fully described in Hjort et al. (2022). The main idea is to visually observe all the different geofeatures, i.e. elements of geology, geomorphology and hydrology, present at a site (all the potential geofeatures are listed in the field form in Online appendix S2). The outcome geodiversity variable is the sum of different geofeatures that are found at each site (i.e., georichness). We observed geofeatures inside a circle of 5 m radius using the vegetation plot as a center point (Hjort et al. 2022). Geodiversity was observed from a slightly larger area

Table 1 Characteristics of the three mountain heath and tundra regions and a description of the studied ecological variables

Region	N. of plots	Dominant habitat types	GP (reindeer/km ²)	Elevation (m.a.s.l.)	Total species richness	Vasc richness	Bryo richness	Lich richness	Calcium (mg/g)*	GDD (°C days)*	Solar radiation (Mwh/m ²)*	TWI*	Empetrum coverage (%)*	Geo- richness*	TH*
1. Iso- lated, low- lying moun- tain heaths	44	Northern boreal Cal- lina, Myr- tillus, and Empetrum types	Low (1–1.5)	455 ± 4 (400– 540)	20 ± 1 (12– 29)	7 ± 0 (3–13)	5 ± 0 (3–10)	8 ± 1 (2–16)	0.4 ± 0 (0.1– 0.8)	525 ± 6 (448– 594)	538 ± 15 (285– 686)	5.7 ± 0.2 (2.9– 8.6)	35 ± 3 (5–85)	4.8 ± 0.3 (1–8)	2 (1–7)
2. Spo- radic moun- tain heaths and tundra	58	Hemi-arctic and arctic Myrtillus, Empetrum, and Betula nana types	Moderate (1.5–2)	494 ± 11 (367– 770)	27 ± 2 (15– 36)	9 ± 0 (5–16)	6 ± 0 (1–11)	12 ± 1 (0–20)	0.3 ± 0.1 (0.0– 2.0)	404 ± 10 (206– 570)	591 ± 53 (497– 692)	6.5 ± 0.2 (4.4– 9.5)	27 ± 2 (0–80)	4.7 ± 0.2 (1–11)	2 (1–9)
3. Con- tinuous moun- tain heaths and tundra	63	Hemi-arctic and arctic Myrtillus, Empetrum, and Betula nana types	High (<2)	641 ± 7 (330– 825)	30 ± 2 (11– 48)	10 ± 1 (4–23)	8 ± 0 (3–14)	13 ± 1 (0–26)	0.6 ± 0 (0.1– 1.9)	273 ± 5 (142– 349)	583 ± 9 (416– 734)	7.0 ± 0.2 (3.8– 9.0)	32 ± 3 (1–90)	4.3 ± 0.2 (1–9)	3 (1–10)

Grazing pressure (GP, reindeer/km²) is calculated as an average of 15 years prior vegetation survey from annual reindeer numbers within reindeer herding districts (Finnish Reindeer Herder's Association 2022). Mean ± std and range (in parentheses) are given for species richness variables, elevation, calcium content, growing degree days sum (GDD), solar radiation, topographical wetness index (TWI), Empetrum cover, and georichness. Median and range (in parentheses) is given for topographical heterogeneity (TH). Used environmental variables in models are marked with *

than species richness, because the geofeatures present in the immediate vicinity of the vegetation plot may influence which species are found from the plot (Hjort et al. 2022). Geodiversity can be considered temporally relatively stable compared to biodiversity (Lawler et al. 2015), thus it is reasonable to assume that the time difference between collecting vegetation data and geodiversity data is insignificant for the results.

Other environmental variables

We recorded other environmental variables that are known to be important for Arctic-alpine species richness alongside geodiversity. We observed meso-scale topographical heterogeneity in the field, by visually estimating the roughness of the plots (radius 5 m). The scale of the heterogeneity measure is from 1 to 10, where 1 refers to very low variation in topography and 10 very high variation (see examples of plots with different levels topographical heterogeneity in Online appendix S6). We calculated topographical wetness index (TWI) based on digital elevation model (DEM) in a 10 m resolution (NLS 2020) with ArcGIS Pro. Based on the DEM, we calculated the annual potential incoming solar radiation (kWh/m³) with ArcGIS tool Points Solar Radiation. We measured the amount of calcium (mg/g) from surface soil samples from the top five centimeters (or less if thinner) of organic soil layer. Soil samples were pooled from 5 samples within vegetation plot. We also estimated the percentage cover of *Empetrum* from the vegetation plot. Growing degree days sum (GDD) was extracted from the data of Aalto et al. (2021) and its resolution is 100 m x 100 m.

Statistical methods

We used non-metric multidimensional scaling (NDMS) ordination to explore the compositional variation of the observed geofeatures and correlated it with vascular plant, bryophyte, and lichen species richness, and their sum or total species richness. Similar to using species data, such an approach can be applied using data on geofeatures (Tukiainen et al. 2022a). Ordinations were made separately for the three study regions based on presences of geofeatures and Jaccard dissimilarity as the distance metric. Correlation vectors of species richness variables

(vascular plant, bryophyte, and lichen species richness, and their sum or total species richness) were fitted to each ordination and their goodness-of-fit was assessed using 999 permutations. The ordinations were done using R package ‘vegan’ (R Core Team 2022; Oksanen et al. 2022; Salminen et al. 2023).

To answer the second study question about how geodiversity explains species richness, we made univariate generalized linear models (GLM) for georichness and four species richness variables (total, vascular, bryophyte and lichen richness) separately for the three study regions. The models were made with Poisson error distributions.

To test whether geodiversity is a meaningful richness predictor among other environmental factors (Table 1), we used generalized linear models with Poisson distribution. We standardized all explanatory variables with z-score standardization method. We built the models separately for each region and used stepwise Akaike information criterion (AIC) selection, which selects the best model based on the AIC value. To test the collinearity between predictor variables, we ran Spearman’s correlation analysis. No alarmingly high correlations ($R_{\text{Spearman}} > 0.7$) were observed (Dormann et al. 2013; Online appendix S3) and therefore, all the environmental variables were included in the models.

Results

Altogether, we found 23 different types of geofeatures from the studied sites. The most common geological geofeature was diamicton (i.e., till), which was found from all the plots in continuous and sporadic mountain tundra (Fig. 2). Physical weathering was the most common geomorphological feature, and dry channel the most common hydrological feature across the studied sites. The study sites in continuous mountain heaths and tundra were characterized by frost and wind related geofeatures, whereas glaciofluvial, fluvial and biogenic features were more pronounced (and in the case of coarse sediment, glaciofluvial, as well as fluvial erosion and deposition were only present) in sporadic mountain heaths and tundra and in isolated low-lying mountain heaths. The amount of detected hydrological geofeatures was low across the regions (Fig. 2).

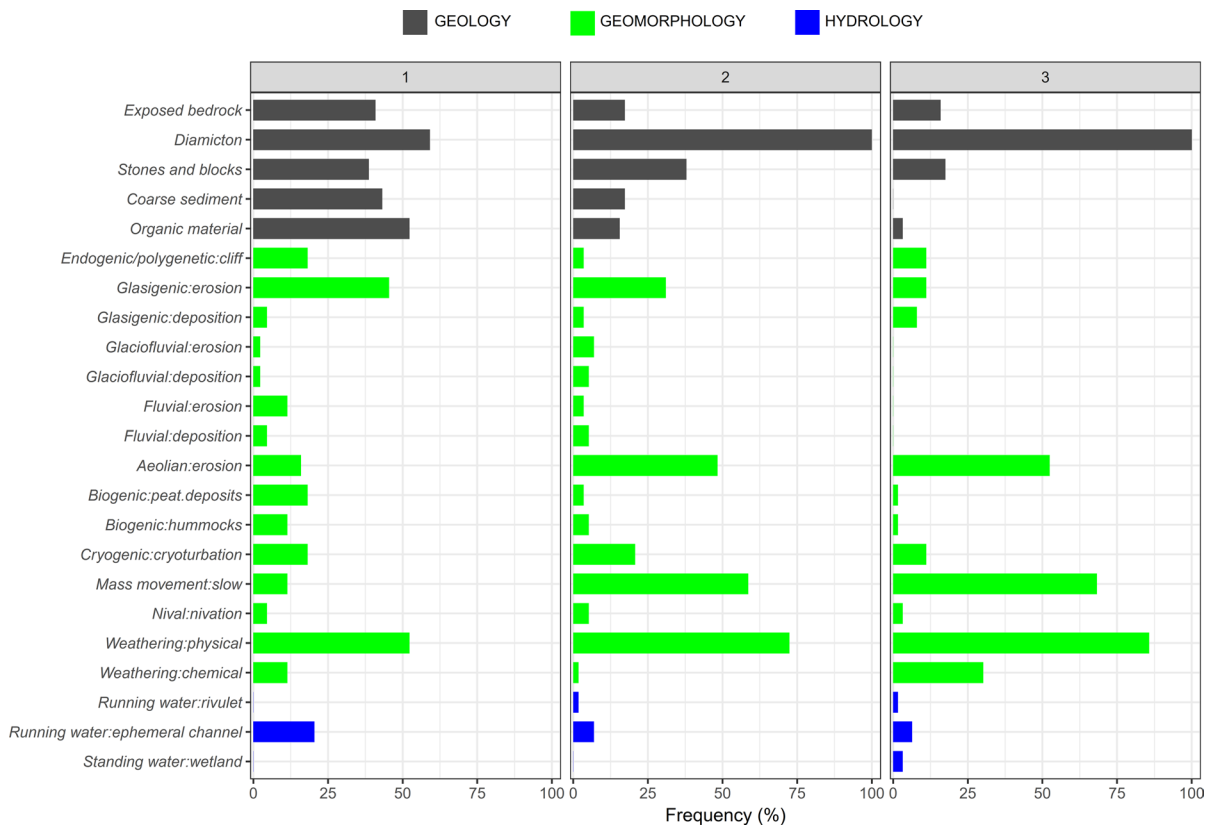


Fig. 2 Frequencies of geofeatures in each mountain heath and tundra region (1 = Isolated low-lying mountain heaths, 2 = Sporadic mountain heaths and tundra, 3 = Continuous mountain

heaths and tundra). Geofeatures were grouped into geological, geomorphological, and hydrological features

According to the NMDS ordination, the composition of geofeatures correlated with vascular plant richness ($R^2=0.25$, $p=0.007$), bryophyte richness ($R^2=0.17$, $p=0.024$) and lichen richness ($R^2=0.44$, $p=0.001$) in isolated low-lying mountain heaths, with vascular plant richness ($R^2=0.11$, $p=0.036$) in sporadic mountain heaths and tundra and with total species richness ($R^2=0.12$, $p=0.029$) and bryophyte richness ($R^2=0.09$, $p=0.044$) in continuous mountain heaths and tundra (Fig. 3). Geofeatures associated with peat tended to correlate with higher vascular plant and bryophyte richness in isolated low-lying mountain heaths and with vascular plant richness in sporadic mountain heaths and tundra. In contrast, lichens seem to thrive when signs of physical weathering, cryoturbation and glacial erosion are present. In continuous mountain heaths and tundra, in turn, ephemeral channels and cliffs were often present when total and bryophyte richness were high.

According to both the univariate and multivariate GLM models, georichness had a statistically significant ($p<0.05$) positive effect on lichen richness in isolated low-lying mountain heaths and all species richness variables in continuous mountain heaths and tundra (Figs. 4 and 5). Of the other significant predictors in multivariate GLMs, solar radiation had positive effect and GDD and topographical heterogeneity negative effect on lichen richness in isolated low-lying mountain heaths, while *Empetrum* cover affected negatively on vascular plant richness (Fig. 5a). In sporadic mountain heaths and tundra, GDD had negative effect on lichen richness (Fig. 5b). Finally, in continuous mountain heaths and tundra, GDD and *Empetrum* cover had negative effect and calcium and TWI positive effect on vascular plant richness. TWI affected positively also on bryophyte richness. Topographical heterogeneity, calcium and TWI had negative effect on lichen richness (Fig. 5c).

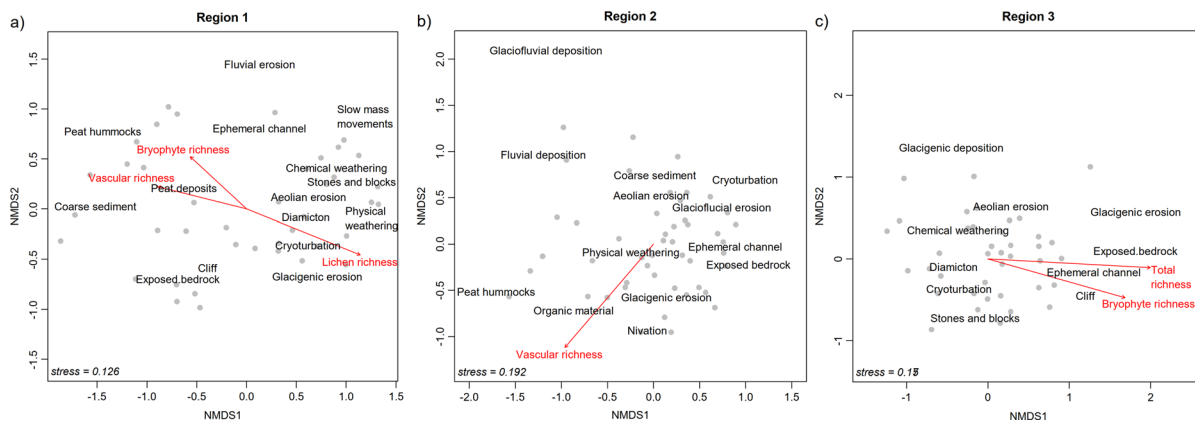


Fig. 3 Non-metric multidimensional scaling (NMDS) ordinations, based on presences of different geofeatures, and their correlation with species richness variables in **a** isolated low-lying mountain heaths (region 1), **b** sporadic mountain heaths and tundra (region 2) and **c** continuous mountain heaths and

tundra (region 3). Only significant ($p < 0.05$) correlations are displayed. Gray dots represent study plots. The 70% most abundant and best fitting geofeatures are displayed for each region and were extracted using R package ‘goevveg’ (von Lampe and Schellenberg 2021)

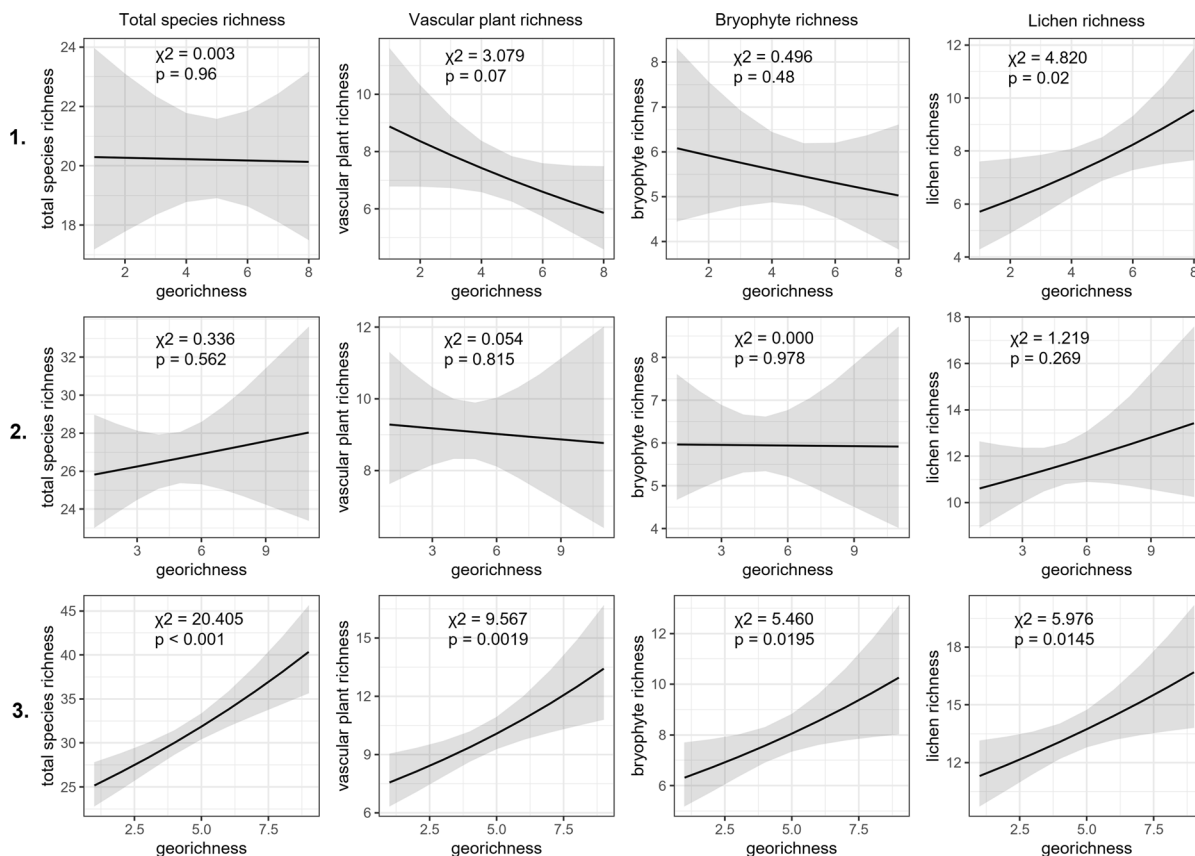


Fig. 4 Univariate generalized linear models for total, vascular plant, bryophyte, and lichen richness in 1. Isolated low-lying mountain heaths, 2. Sporadic mountain heaths and tundra, and 3. Continuous mountain heaths and tundra

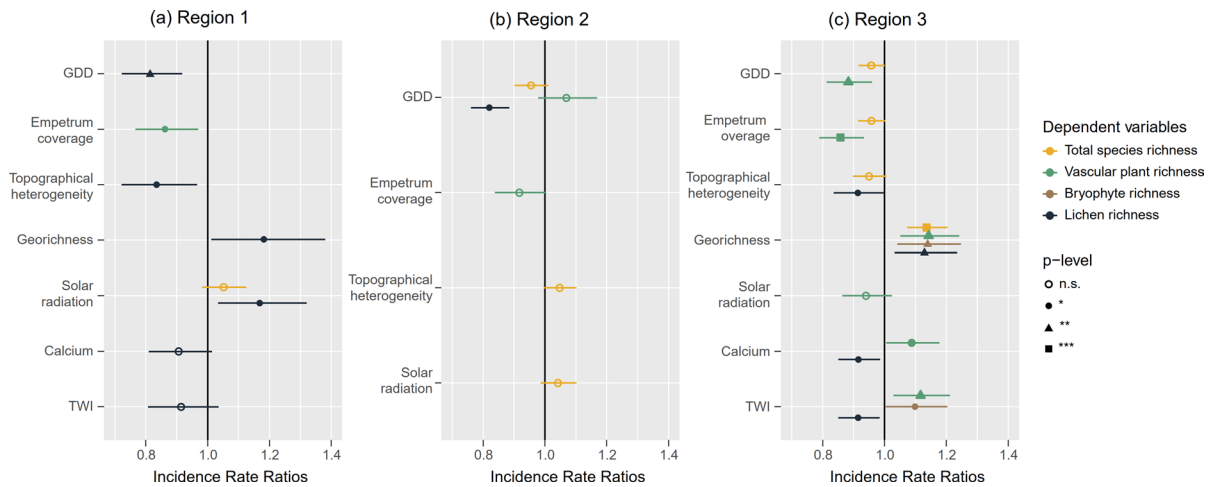


Fig. 5 Forest plots showing environmental variables of the best generalized linear model made for total, vascular plant, bryophyte, and lichen richness in **a** Isolated low-lying mountain heaths (Region 1), **b** Sporadic mountain heaths and tundra (Region 2), and **c** Continuous mountain heaths and tundra (Region 3). Estimates are incidence rate ratios with 95% confidence intervals

dra (Region 2), and **c** Continuous mountain heaths and tundra (Region 3). Estimates are incidence rate ratios with 95% confidence intervals

Discussion

Geodiversity has been positively related to biodiversity in several studies using coarse scale data (Tukiainen 2022b), but little is known about whether this relationship holds true when fine-scale environmental data are used. We studied how plot-scale geodiversity is linked to vascular plant, bryophyte, and lichen species richness, as well as their sum (total richness) in three mountain heath and tundra regions. Our results show that the composition of geofeatures correlates with species richness variables in each study region. We also found evidence that plot-scale georichness is positively associated with different species richness variables in two of the study regions. Indeed, the positive association between geodiversity and all species richness variables was evident in continuous mountain heaths and tundra, and lichen richness and geodiversity were positively correlated also in the isolated low-lying mountain heaths. These findings lend partial support for our hypothesis that plot-scale geodiversity and species richness are positively associated across high-latitude landscapes, also when other significant ecological determinants are included in the analyses. Our findings indicate that geodiversity can have additional importance for species richness models beyond well-known environmental variables explaining high-latitude vegetation patterns.

Geodiversity is meaningful for plot-scale species richness

In this study, we considered geodiversity both qualitatively as individual geofeatures, as well as quantitatively as georichness that was the total number of different geofeatures at each site. Combining qualitative and quantitative methods might provide more comprehensive interpretation on geodiversity's characteristics and importance for biodiversity (Gonçalves et al. 2022) but is rarely done to date. Examining the geofeature composition (or "geocomposition") of the study sites by using distance-based ecological methods can provide new insights to understanding what kind of geocomposition or which geofeatures are related to species diversity (Tukiainen et al. 2022a). We found connections between geocomposition and species richness in each study region. The presence of organic material (peat) seems to increase vascular plant and bryophyte richness in isolated low-lying mountain heaths and vascular plant richness in sporadic mountain heaths and tundra. This is likely due to the establishment of species typical to peatlands that would not otherwise be found in mountain heaths and tundra. In continuous mountain heaths and tundra, the presence of ephemeral channels, exposed bedrock and cliffs were linked to

total and bryophyte richness. The presence of water is known to be important for species richness in the tundra (Kempainen et al. 2019), in this case as run-off along seasonal streams or along cliffs (that are also closely related to exposed bedrock), providing microhabitats with higher soil moisture. These results not only give insights which specific geofeatures could be important for species richness in mountain heaths and tundra but also demonstrates how quantitative geodiversity information can be applied to understand species richness patterns.

Georichness was positively connected with all species richness variables in the northernmost study region, in continuous mountain heaths and tundra. The importance of georichness for species richness in this region may be explained by the relatively large species pool of the region (see Table 1 and Online appendix S1). Simply, there are more potential species to inhabit the niches that become available by the increasing geodiversity compared to the southern regions where species pool is smaller. Moreover, long-term evidence shows increasing shrub abundance in the isolated boreal mountain heaths (Maliniemi et al. 2018; Maliniemi and Virtanen 2021). This may complicate observing the potential positive link between geodiversity and biodiversity as shrubs are strong competitors that may occupy the available niche space and have negative effect also on species richness. Lichens were the only species group having a positive, although not always significant, relationship with georichness in each region. Lichens favor dry and often relatively barren growing conditions (Jonasson 1981), which are characteristic to the majority of the geofeatures in our data (such as glacial erosion, aeolian erosion and physical weathering). Varying associations between species richness and georichness indicate that their connection might be context-dependent—for instance, dependent on the species group, or the location of the observations. It is also possible that in some cases, the importance of other environmental variables may override the effect of geodiversity in explaining species richness (as suggested also e.g. by Toivanen et al. 2019).

The effects of other environmental variables on species richness were mostly in line with the previous knowledge. The cover of *Empetrum* had a systematic negative impact on vascular plant species richness across our study regions. *Empetrum* is mechanistically and chemically strong competitor that interferes

and suppresses other plants allelopathically (Bråthen et al. 2010), and our results add to the existing, yet not many empirical, evidence of its negative effect on tundra species richness (le Roux et al. 2014; Mod et al. 2016). As *Empetrum* cover has increased in many mountain heath and tundra sites over decades (Maliniemi et al. 2018), including it to species richness models becomes increasingly important. Soil moisture conditions, estimated using TWI, affected species richness as expected, as the availability of water is a key factor determining species growth in arid mountain tundra ecosystems (Kempainen et al. 2019). Lichens were negatively associated with TWI in continuous mountain heaths and tundra and isolated low-lying mountain heaths, whereas vascular plant and bryophyte richness had positive associations with TWI. Alkalinity of soils and rocks boost plant growth and enable species to establish vital populations (van der Welle et al. 2003; le Roux et al. 2014), and the amount of calcium is known to be an important determinant for species richness in northern environments (Gough et al. 2000; van der Welle et al. 2003). We found calcium concentration to be positively associated with vascular plant species richness in continuous mountain heaths and tundra. However, calcium had negative effect on lichen richness. This may be related to its positive effect on vascular plants, not only in relation to richness but also biomass that may further have negative impact on lichen abundance (Cornelissen et al. 2001). Similar to the effect of calcium, the negative effect of GDD on lichen richness on isolated low-lying mountain heaths and sporadic mountain heaths and tundra may be explained through its positive effect on vascular plant biomass, i.e., at treeline ecotone, sites with higher GDD may be too dense for lichens. GDD can be seen to some extent as a counter part of the other energy-related variable, freezing degree days (FDD), that have been proved to have positive relationship with lichens and vascular species richness (Niittynen et al. 2020). The amount of solar radiation is high on mountain tops, where also lichens are most abundant in the southernmost study region and may thus be positively linked to lichen richness. The negative effect of topographical heterogeneity on lichens is, in turn, harder to explain, as other studies have reported opposing effects (Bruun et al. 2006; Zelený et al. 2010). Nevertheless, our results clearly show (Online appendix S3) that meso-scale topographical heterogeneity does

not correlate significantly with georichness, and thus is not equal to geodiversity which is sometimes a subject of confusion.

Geodiversity adds value to ecological approaches and biodiversity management

Our findings from mountain heath and tundra environment indicate that geodiversity has additional explanatory power over and above the traditionally used environmental variables, such as GDD and calcium concentration in soil, in explaining species richness patterns. Previously, inclusion of geodiversity has improved species richness models in northern environments, e.g. across Finnish national parks (Tukiainen et al. 2017b) and in Great Britain (Bailey et al. 2017). Our results are in-line with these landscape-scale findings and give valuable additional information on the plot-scale connections between geofeatures, georichness, and species richness of multiple species groups in mountain heath and tundra environments. Georichness seems to capture abiotic variation that is not reached by other environmental variables of this study, especially in continuous mountain heaths and tundra. Within this study set-up, it is not possible to determine the exact processes and mechanisms behind the positive effect of geodiversity on species richness, but they are likely linked to variation, for example, in microclimatic conditions and in the soil properties. Further studies should explore what are the mechanisms behind observed positive link between geodiversity and species richness.

Regardless of the mechanisms behind the positive geodiversity-biodiversity relationship, information on plot-scale geodiversity could be applied in the management and conservation of mountain heath and tundra environments. Biodiversity of these northern environments is vulnerable to the effects of the fast-changing climatic conditions, and it would be essential to find complementary strategies for its conservation during the upcoming years (IPBES 2019; Aronsson et al. 2021). According to our study, information on plot-scale geodiversity could be used, for example, as a coarse-scale estimate of species richness in continuous mountain heaths and tundra (Haapasaari 1988), following the idea that geodiversity provides heterogenic platform for biodiversity to thrive (Beier et al. 2015). As the connection between geodiversity and biodiversity may be

context-dependent, we encourage for further plot-scale explorations across the circumpolar heaths and tundra, as well as in other ecosystems. Furthermore, it is important to gain knowledge on the variation of abiotic features in heath and tundra environments, as climate change can also alter certain geofeatures (such as frost-related landforms and processes) and thereby, influence plant community properties (Kemppinen et al. 2022).

There is a growing interest in exploring and applying complementary biodiversity conservation approaches, such as conserving nature's stage (CNS) strategy, in conservation planning (Lawler et al. 2015; Zhu et al. 2022). By continuing to monitor the sites, this study lays the groundwork for future testing of this strategy, that aims to maintain sites with high species diversity over time. In addition, our study supports the qualitative approach in geodiversity assessments (Zwólinski et al. 2018), or that the quality of geodiversity (i.e., what are the geofeatures that geodiversity of each site consists of) should also be considered in ecological approaches. This is especially important when using geodiversity in conservation approaches, and when evaluating the application of CNS at local scales.

Conclusions

We showed that plot-scale geodiversity has positive, yet context-dependent relationship with species richness in mountain heaths and tundra landscapes. Geodiversity supports species richness in continuous mountain heaths and tundra and lichen richness in isolated low-lying mountain heaths. This has implications especially for biodiversity management, where geodiversity could be applied as a coarse-scale estimate of species richness. Our results also demonstrate that an integrated approach including both quantitative (georichness) and qualitative (geofeatures) approaches to study the effect of geodiversity on species diversity could benefit biodiversity management. However, as this study is among the first ones to explore the plot-scale relation between geodiversity and biodiversity, there is a need for further investigations which explore how plot-scale geodiversity and species richness, as well as other measures of biodiversity, are connected across areas and environments.

Acknowledgements HT, JA, and TM were supported by the Academy of Finland (Project Number 322652), TM also by the Finnish Cultural Foundation and KH by the Ella and Georg Ehrnrooth Foundation. We would like to thank Henna Snåre and Petteri Kiilunen for their input on collecting the plot-scale geodiversity data and Tarja Törmänen for making the calcium analyses. Special thanks to S-Market Salla for helping in serious challenges with freezers that were needed to keep our soil samples cold.

Author contributions TM, JH & JA conceived the idea; Field work was conducted by HS (geodiversity), KH (soil samples), TM, JK & RV (vegetation); HS, TM & LCP-R analyzed the data; HS led the writing with assistance of TM & HT; All authors contributed critically to the drafts and gave final approval for publication.

Funding Open Access funding provided by University of Oulu including Oulu University Hospital. HT, JA, and TM were supported by the Academy of Finland (project number 322652), TM also by the Finnish Cultural Foundation and KH by the Ella and Georg Ehrnrooth Foundation. The research leading to these results has received funding from the European Union's Horizon 2020 project INTERACT, under grant agreement No 730938.

Data and code availability The data and code that is used in this study has been deposited in a Zenodo data repository (Salminen et al. 2023) <https://doi.org/10.5281/zenodo.7602641>.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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