The role of geodiversity in providing ecosystem services at broad scales

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HIGHLIGHTS

- Geodiversity was mainly positively related to ecosystem services (ESs)
- Geodiversity complemented biodiversity in explaining ESs
- Geodiversity should be more deeply integrated into ES research

ABSTRACT

Mapping of ecosystem services (ESs) provide valuable information on the geographical variation of ESs and their relation to overall diversity. Although the relationship between biodiversity and ESs has been intensively explored, little is known how geodiversity (i.e., variety of geological, geomorphological and soil features) is associated with different ESs. We studied 1) the spatial variation of geodiversity and biodiversity in relation to six ESs (i.e., forest carbon budget, potential supply of groundwater, milk and meat production, crop production, amount of free-time residences and nationally valuable landscapes) using variation partitioning (VP), and 2) the spatial overlap between geodiversity and biodiversity and ESs using generalized additive models (GAM) in 1006 intensively surveyed grid cells of 100 km^2 located across Finland. In the VP, biodiversity independently explained more of the variation than geodiversity for majority of the ESs. However, shared explanation ability of biodiversity and geodiversity was considerable for majority of ESs (forest carbon budget: 41.3%, crop production: 15.0%, free-time residences: 15.2% and valuable landscapes: 7.3%), often exceeding that of both independent contributions. GAMs indicated that increase in both biodiversity and geodiversity enhances forest carbon budget (D^2 = 66.8% and 12.4%, respectively), potential production of groundwater (8.3% and 0.1%), crop production (35.7% and 8.9%), free-time residences (40.0% and 7.9%) and valuable landscapes (11.6% and 6.9%). However, the positive relationship between diversity and ESs levelled off for many of the ESs. Our findings suggest that geodiversity is an important complementing factor in explaining spatial variation of the ESs in high-latitude regions. We also found dominantly synergic effects between abiotic diversity and ESs. Thus, our study results highlight the need to more deeply incorporate abiotic diversity into ESs research. Environmental conservation and management would benefit from the more comprehensive integration of geodiversity to ESs research along with the changing environmental conditions of future decades.

Keywords: Biodiversity, Boreal, Ecosystem service trade-off, Geodiversity; High-latitude; Mapping of ecosystem services, Spatial

1. INTRODUCTION

Ecosystems provide various goods and services to mankind, thus contributing through these ecosystem services (ESs) to human well-being and economic wealth (Millennium Ecosystem Assessment 2005; Anderson et al. 2009; Morelli et al. 2017; Dobbs et al. 2018; Li and Wang 2018). ESs are fundamentally linked to biodiversity, which can be, depending on the definition, a regulator of ESs, a final ESs or a good (Mace et al. 2012). One approach to study this relationship between biodiversity and ESs has been to map the spatial variation between biodiversity and ESs at different scales (Naidoo et al. 2008; Anderson et al. 2009; Holt et al. 2016). However, biodiversity (i.e., biotic diversity) is only another half of (overall) diversity, composing also of abiotic (i.e., inanimate physical nature) component, and inclusion of this abiotic diversity has been largely neglected in the previous mapping studies (Gray 2013; Lawler et al. 2015; Bailey et al. 2017; Tukiainen et al. 2017a, 2017b). Hence, more emphasis should be focussed on investigating how abiotic diversity and ESs are related at different spatial scales (e.g., Gray 2012; Gordon and Barron 2013; van Ree and van Beukering 2016). This lack of research is also associated with ecosystem multi-functionality, as abiotic diversity can deliver combinations of a variety of overlapping functions, each of which delivers different ESs to society (Lee and Lautenbach 2015). These overlapping functions can yield synergetic or trade-off effects between diversity patterns and ESs, suggesting which ESs people may either get (synergic) or lose (trade-off) at a certain time (Rodrigues et al. 2006; Mastrangelo et al. 2014; Lee and Lautenbach 2015). However, no previous study has considered whether the relationship between abiotic diversity, in addition to biodiversity, and multiple ESs provide synergic or trade-off effects at broad scales.

Understanding how diversity patterns of abiotic features influence on and shape surrounding environment has gained wider interest only recently (Benito-Calvo et al. 2009; Hjort and Luoto 2010;

Gordon et al. 2012; Gray 2013; Pereira et al. 2013; Pellitero et al. 2015). These abiotic features are referred as geodiversity, which is commonly defined as the variety of geological (rocks, minerals, fossils), geomorphological (land form, processes), and soil features (Gray 2008; 2013). Geodiversity as the abiotic equivalent of biodiversity provides the basis upon which living creatures from plants to human exist and interact, thus connecting people, nature, landscapes and cultural heritage in a holistic manner (Gordon and Barron 2013; Matthews 2014; Lawler et al. 2015). Geodiversity also underlies the aesthetic value of landscapes and contributes to sustainable economic development and benefits public health by providing opportunities for outdoor recreation (Gordon and Barron 2013; Gray 2013). Although, it has been recognized, through the continued interaction with natural processes and the implementation of integrated approaches in land and water control and conservation, that geodiversity strongly contributes to sustainable environmental management and decision-making (Gordon and Barron 2013; Gray 2013; Hjort et al. 2015), it has only recently been more widely accepted to the ESs framework (van Ree and van Beukering 2016; CICES 2018).

Despite the lack of recognition during the past in the ES framework, geodiversity is intimately related to ESs. It contributes to every ESs categorization from provisioning, and regulating and maintaining services to cultural services (CICES 2018), thus having a crucial role in providing benefits to society. For example, abiotic environment provides habitat for biota combination with biotic and cultural resources, fresh water and mineral resources, regulates climate conditions, controls hydrology and erosion, facilitates nutrient cycling and enhances recreation and ecotourism (Gray 2013; Gordon and Barron 2013; van Ree and van Beukering 2016; Bailey et al. 2017; CICES 2018). Although the link between geodiversity and ESs is evident and ESs definitions recognize that an ecosystem includes the abiotic component of habitat, most published empirical case studies on ESs refer entirely or mainly on services originated exclusively from biodiversity (Gray 2013; but see Gordon and Barron

2013). This shortage of individual studies hinders our possibilities to comprehensively understand beyond conceptual perspectives the relationship between geodiversity and ESs.

Our focus is to determine 1) the spatial variation of geodiversity and biodiversity in relation to six ESs (i.e., forest carbon budget, potential supply of groundwater, milk and meat production, crop production, amount of free-time residences and nationally valuable landscapes), and 2) the spatial overlap between geodiversity and biodiversity and ESs in Finland at broad scale (10 km resolution). For the spatial overlap, we focussed on the geo-biophysical constraints (i.e., geodiversity and biodiversity) that may promote (synergy; e.g. monotonically increasing or non-linear positive relationship), limit (trade-off) or have no effect (no-effect) in delivering the six ESs (following the terminology of Lee and Lautenbach 2016), without considering social or economic constrains or relationships among the ESs itself (see Cavender-Bares et al. 2015). We founded our spatial overlap hypothesis on a simplified interpretation how changes in diversity (i.e., both biodiversity and geodiversity) are predicted to affect three types of ecosystem services (de Groot et al. 2010; Science for Environment Policy 2015; Fig. 1). For regulating services (forest carbon budget and potential supply of groundwater in our study), enhancing diversity typically increases the degree of services, but the pattern varies in the highest diversity environments depending on the type of service. For provisioning services (milk and meat production, and crop production), no services exist in pristine environments, because ecosystem needs to be at least temporarily disturbed in order to obtain provisioning services from nature. In lowering diversity with increasing intensity of use, more provisioning services are only gained by adding human input (e.g., fertilizer, water or labour) to ecosystem. The production of provisioning services finally diminishes as diversity clearly decreases in monotonic urban-like environments. Cultural services are separated to two different ones. For cultural-recreation services (amount of free-time residences), a crucial feature in valuing these services is accessibility, because pristine systems are often inaccessible. Thus, increased accessibility leads to more active use of cultural services until a subsequent drop in service value is reached in highly remote systems. For cultural-information services (nationally valuable landscapes), increase in diversity increases also this service value.

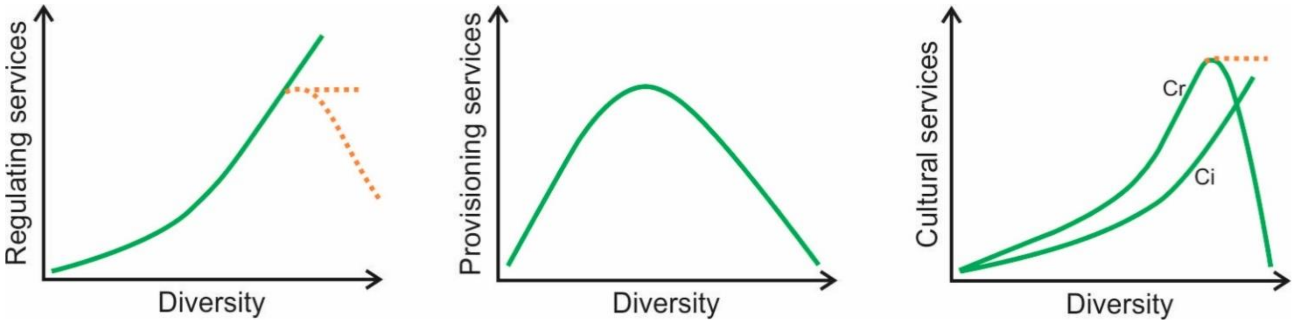

Fig. 1. Conceptual illustration of the relationship between diversity (i.e., biodiversity and geodiversity) and ecosystem services (ESs) (Cr: sum of cultural-recreation value, Ci: sum of cultural-information value including aspects such as cultural heritage and education). Broken lines indicate alternative patterns for geodiversity depending, for example, on studied region and magnitude of human pressures (Gordon and Barron 2013; Gray et al. 2013). The patterns are partly based on Science for Environment Policy (2015). However, there is no comprehensive empirical evidence existing how geodiversity and ESs are related. Moreover, the relationships are tentative and specific situations will have specific versions of these generalized curves. Both the shape of these curves and the magnitude of the different corresponding ESs levels determine the shape of the overall ESs level curve and whether an overall optimum can be reached (de Groot et al. 2010).

2. MATERIAL AND METHODS

2.1 Study area

The study area consisted of 1006 100 km^2 grid cells that were dispersed across Finland, located in northern Europe approximately between 60° and 70° N and between 20° and 31° E (Fig. 2). Grid cells containing more than 80 per cent of land area (i.e. maximum of 20% water areas) were included in the study. The total land area of Finland is 303 891 km^2 with the population of 5.5 million. Finland formed a good model environment to study the relationship between geodiversity and ESs, because variable geological and geomorphological exist and detailed information on the particular ESs were available there. In addition, human disturbance is relatively modest in Finland compared to many other countries, enabling us to investigate geodiversity and biodiversity in more natural settings.

Moreover, it is important to study high-latitude environments, which are especially sensitive to climate warming (Vilmi et al. 2017).

2.2 Geodiversity and biodiversity

Geodiversity variables, i.e. geomorphological, soil and rock richness, were assembled following Hjort and Luoto (2010, 2012, Table 1). Geomorphological richness was measured using landform observations, GIS-based environmental variables and generalized additive modelling (see Supporting Information for details, Tukiainen et al. 2017a), and calculated as the mean of landform types in each grid cell (Fig. 2). Soil and rock richness were counted by summing the number of different soil and rock types in each grid cell separately. Soil types were derived from a digital soil map, in which soil was divided into eight classes: 1) rock (bare rock or thin soil cover; < 1 m), 2) till (glacigenic deposits), 3) stony areas and block fields, 4) sand and gravel, 5) silt, 6) clay, 7) gyttja (lake and sea sediments; > 6 % organic material), and 8) peat. Rock types were determined using a digital bedrock map,. For exploring the spatial overlap between geodiversity and ESs a compound measure of geodiversity ('total georichness') was computed by summing the standardized values of geomorphological, soil and rock richness.

Biodiversity variables consisted of the total number of vascular plant, nesting bird and butterfly (Macrolepidoptera) species recorded in each 10 x 10 km grid cell (Fig. 2). These data sets are widely used in the research (e.g., Kivinen et al. 2008) and they are the best available data on these biological assemblages covering the whole country (Table 1). We focused on total biodiversity instead of e.g. threatened species, of which vascular plants and butterflies have been studied elsewhere (Tukianen et al. 2017a), to maintain comparability with the (total) geodiversity. The vascular plant data comprised the presence records of all observed vascular plant species in each inventoried grid cell (subspecies and hybrids were excluded). Only comprehensively mapped grid cells were included into the dataset. The nesting bird data consisted of professional- and voluntary-based observations of nesting birds across the Finland. The used data comprised the presence records of all nesting birds in each grid cell. The butterfly data was based presence observations per each grid cell with observations made by professional and volunteer amateur lepidopterists using a uniform 10610 km^2 grid system across the Finland. A measure comparable to the total georichness (i.e. 'total species richness') was computed by summing the standardized values of vascular plant, nesting bird and butterfly richness.

Table 1. Summary of the geodiversity, biodiversity and ecosystem services (ESs) variables used in the study. All the variables were upscaled to the resolution of $100 km^2$. See detailed information about the variables in the text.

	Original resolution	**Survey period**	**Values per 100 km^2 grid cell (mean/min-max)**	**Value unit**	**Maintained by**	**Reference**
Geodiversity variables						
Geomorphological richness	1 km^2	-	5.2 (3-11)	Richness	University of Oulu	Hjort & Luoto 2010, 2012; Tukiainen et al. 2017a: Supporting Information
Soil richness	$1km^2$	-	5.6 (2-8)	Richness	Geological Survey of Finland, University of Oulu	GSF 2010a, Tukiainen et al. 2017a

Rock richness	$1km^2$	-	3.9 (1-10)	Richness	Geological Survey of Finland, University of Oulu	GSF 2010b, Tukiainen et al. 2017a
Biodiversity variables						
Vascular plants	$100km^2$	1980-2011	367 (111-1178)	Richness	Finnish Museum of Natural History	Lampinen & Lahti 2015
Nesting birds	$100km^2$	2006-2010	85 (7-153)	Richness	Finnish Museum of Natural History	Valkama et al. 2011
Butterflies	$100km^2$	2001-2011	144 (1-756)	Richness	Finnish Museum of	

					Natural History	
Ecosystem services						
Forest carbon budget	1:25 000	2013	3828 (15-6333)	10 kg C ha-1	Multi-Source National Forest Inventory	Tomppo et al. 2014
Potential supply of groundwater	1:20 000	2013	3328 (0-71000)	m^3/d	Finnish Environment Institute	http://metatieto.ymparisto.fi:8080/geoportal/
Milk and meat production	Actual location of farms	2012-2013	4017 (0-64028)	GJ		Luke 2016; OSF 2016
Crop production	1:20 000	2012	4373 (0-43533)	GJ/ha	Natural Resources	Luke 2012, 2014; Fineli 2018

					Institute Finland, Agency for rural affairs	
Free-time residences	250m x 250m	2014	189 (0-2321)	Number of	Statistics Finland	OSF 2014
Valuable landscapes	$100 km^2$	1995	3.7 (0-99.8)	km^2	The Finnish Ministry of the Environment (managed by the Finnish Environment Institute)	Ala-Hulkko et al. 2016

2.3. Studied ecosystem service variables

In this study, we considered six different ESs which belong either regulation and maintenance, provisioning or cultural ESs, following CICES V4.3 (Haines-Young and Potschin, 2013, Mononen et al. 2016). We used these six ESs variables, because they represented different ESs sections and reliable information was available for these variables on the national scale. Forest carbon budget and potential supply of groundwater both represent regulation and maintenance services. Milk and meat along with crop production belong to the provisioning services and amount of free-time residences together with nationally valuable landscapes are classified to cultural services. For our conceptual study approach (Fig. 1), we distinguished cultural services to two different categories based on Environment Policy (2015): cultural-recreation and cultural-information services.

Forest carbon budget (10 kg C ha-1) was estimated using the carbon stock of biomass as a proxy variable (Fig. 2, Table 1). We used only forest carbon budget in our study, because 72% of Finland's surface area is covered by forests. Spatially explicit biomass estimates were derived from the Multi-Source National Forest Inventory (hereafter MS-NFI) dataset from year 2013. The MS-NFI forest resource maps are based on the NFI field plot data, satellite images and digital maps using a non-parametric k Nearest Neighbours estimation (Katila and Tomppo, 2001; Tomppo et al., 2008). The total tree biomass in forest land was calculated by summing up the biomass estimates of Scots pine, Norway spruce and deciduous forests. The carbon content was assumed to be 50% of the biomass.

Potential supply of groundwater (m^3/d) includes those groundwater areas that are investigated and classified for the water supply purposes (Fig. 2, Table 1, Supporting Information). The dataset includes boundaries of groundwater areas, groundwater recharge areas and sub-areas as well as classifications and information about possible protection plans.

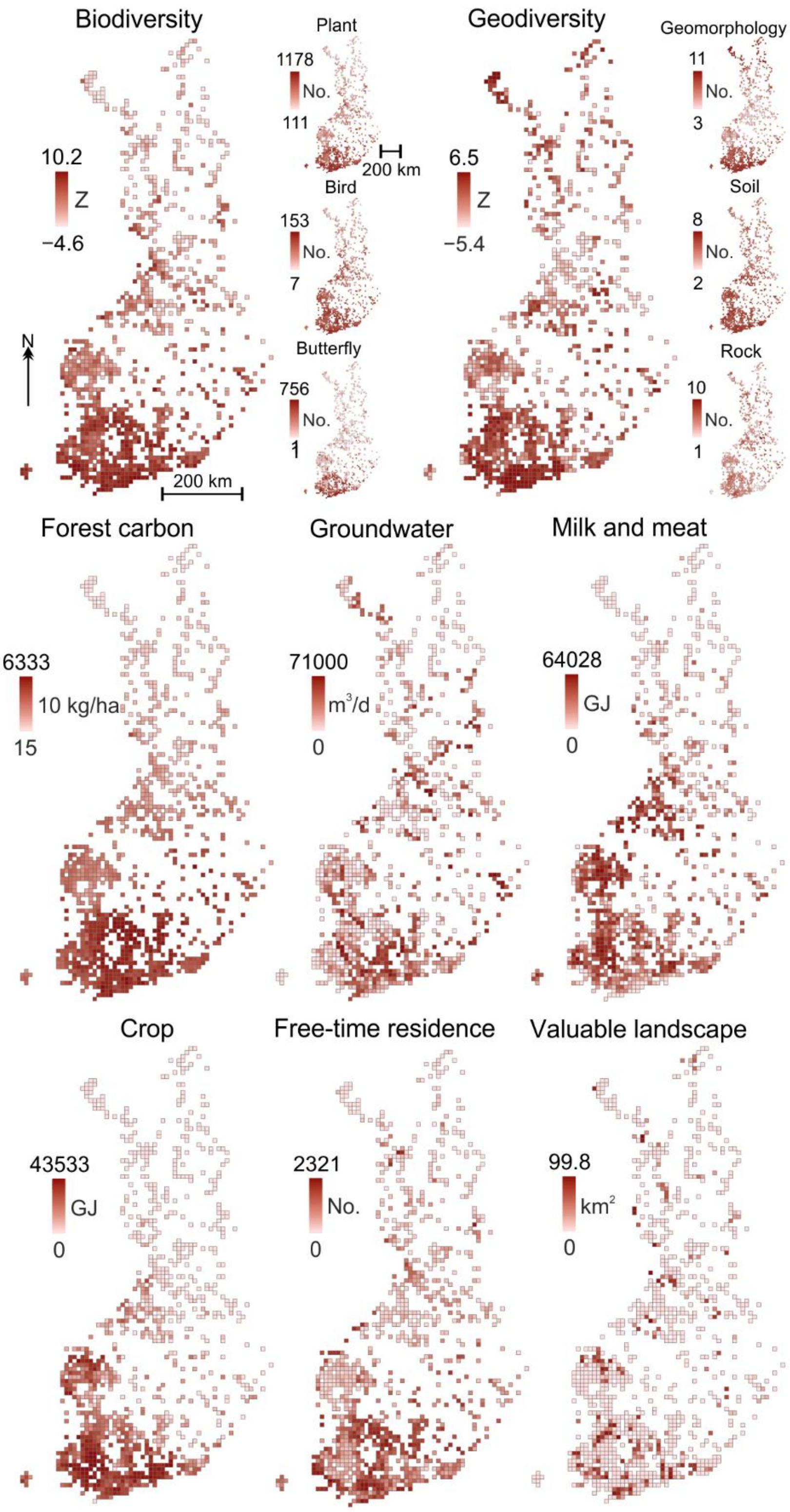

Fig. 2. Spatial distribution of biodiversity, geodiversity and ecosystem services in 1006 studied grid cells (10 x 10 km) found across Finland.

Crop production was mapped according to the capacity of field plots to provide a food service (Supporting Information). The capacity to provide crops is calculated based on Finnish field plot register (Table 1). In addition, there is information on the location and size of fields in the register.

Only crops which were mainly used for food production (≥40 %) were chosen in the study, because the majority of the crop yield is used as animals' feed and industry (Supporting Information). Such crops are potato (51% of yield has been used to production of the food in year 2012), wheat (45%) and rye (93%). The percentage values are based on the statistics of the Balance Sheet of Food Commodities in 2012 (Luke 2012). The information of crop yield (kg/ha/year) has been obtained from Luke (2014). For better comparability the crop yield has been converted into the energy units (GJ/ha). The information for Finnish food nutrient values was obtained from food product register of *Fineli* (managed by National Institute for Health and Welfare, Fineli 2017). Food energy provision per 10 x 10 km was finally calculated by proportioning the year 2012 crop yield (GJ/ha) to overall field area of each crop.

The milk production (GJ) was based on the data which contain information about the number of producers as well as milk production volumes (liters) from years 2012 and 2013 (Fig. 2, Table 1, Supporting Information), respectively (Luke 2016, OSF 2016). The statistics contain information also on-farm usage volumes and the average yield of dairy cows. The meat (pork and beef) production statistics contain information on slaughter volumes (number of carcasses and weight in kilos) and average carcass weights (OSF 2016) from years 2012 and 2013. The mean production values of milk and meat were converted to energy units (GJ) to represent final ESs. GJ values were calculated based on the Fineli (2017). We combined milk and meat production to a single variable, because their geographical variation is more restricted to farm houses.

Amount of free-time residences consisted of geographical statistics on 500,400 existing free-time residences in each grid cell for year 2014 (Fig. 2, Table 1, Supporting Information, OSF 2014). A free-time residence refers to a residential building intended for free-time use that is permanently constructed or erected on its site, or to a residential building that is used as a holiday or free-time dwelling (OSF 2014). The statistics describe the existing stock and number of buildings and free-time residences, excluding for example rental holiday cottages (OSF 2014).

Nationally valuable landscapes or places, which have high historical or cultural value on maintenance(Supporting Information), were officially inventoried in Finland in 1995 based on a decision by the Finnish Ministry of the Environment (Fig. 1, Table 1). The GIS data on nationally valuable cultural environments (managed by the Finnish Environment Institute) consist of data layer on culturally valuable natural diversity, traditional architecture and cultivated agricultural landscape polygons (n = 156 in total, the size of the areas varies between 0.005 and 4 km^2, Ala-Hulkko et al. 2016). Landscapes are protected by means of legislation and collaboration between environmental and cultural administrations.

2.4. Statistical analysis

Partial generalized linear model (GLM, McCullagh and Nelder, 1989) analyses (i.e. variation partitioning, VP, Borcard et al., 1992) were used to study the spatial variation of biodiversity, geodiversity and six ESs across Finland (n = 1006). We applied the approach of Hawkins et al. (2003) in which the coefficients of determination [here D^2 = (null deviance – residual deviance) / null deviance] was used to determine the independent and shared contributions of the explanatory variables. Thus, for each response (i.e. ESs) variable we calibrated three GLMs and computed D^2 using biodiversity variables (vascular plant, nesting bird and butterfly species richness), geodiversity variables (geomorphological, soil and rock richness) and variables from both groups. Based on D^2

values extracted from these three separate GLM runs, we calculated the independent and shared fractions for the two explanatory variable groups. VP analysis with two groups produced four fractions: (i) the independent effect of biodiversity variables, (ii) the independent effect of geodiversity variables, (iii) the shared effect between the two variable groups, and (iv) unexplained variation not captured by independent or shared components (Hawkins et al., 2003). Due to the relatively large sample size GLMs were calibrated using a step-wise Bayesian information criterion (BIC) approach, with standard *glm* function in R (The R Project for Statistical Computing, 2017).

Generalized additive models (GAM) were employed to examine spatial overlap between (i) geodiversity (i.e., total georichness) and ESs, and (ii) biodiversity (i.e., total species richness) and ESs. More precisely, univariate model-based response curves were used to determine the diversity–ESs relationships. GAMs are useful for developing realistic response curves because they fit non-parametric smoothers to the data without requiring the specification of any particular mathematical model to describe nonlinearity (Hastie and Tibshirani 1990). GAM was performed using the *mgcv* package of R (Wood 2011). We calibrated the GAMs using standard *gam* functions and either a Gaussian or Gamma (with an identity or a log link function) error distribution in the model fitting. The family and link function were determined based on exploration of residuals and generalized cross validation score of the models (Wood 2006, 2011). To explore potential nonlinear relationships, the explanatory variable was fitted to the ESs using a smoothing spline with the degrees of freedom permitted to vary between one (i.e. straight-line relationship) and three.

3. RESULTS

3.1. Spatial variation of biodiversity, geodiversity and ESs

Spearman bivariate correlations (R_s) showed that all three biodiversity variables correlated positively to number of ESs (i.e., forest carbon budget: R_s = 0.55-0.78, crop production: R_s = 0.51-0.66, and free-time residences: R_s = 0.52-0.73, Table 2). In addition, these three biodiversity variables were in positive relationship with soil richness (R_s = 0.36-0.52), and butterflies were also related to geomorphological richness (R_s = 0.43). Of the geodiversity variables, only soil richness was markedly correlated with forest carbon budget (R_s = 0.55), crop production (R_s = 0.62) and free-time residences (R_s = 0.40). It should also be noted that rock richness (rockS) was not related to other geodiversity variables (i.e., geomorphologyS and soilS).

Table 2. Spearman bivariate correlation matrix among the studied variables. ** Correlation is significant at the 0.01 level (2-tailed). S associated with the biodiversity and geodiversity variables refers to the richness of a particular variable. See details in Material and Methods.

	PlantsS	BirdsS	ButterfliesS	GeomorphologyS	SoilS	RockS	Carbon	Groundwater	Milk&Meat	Crop	Free-time res.	Landscapes
PlantsS	1	0.748**	0.676**	0.387**	0.518**	0.041	0.780**	0.281**	0.238**	0.641**	0.731**	0.276**
BirdsS		1	0.551**	0.240**	0.503**	-0.033	0.711**	0.290**	0.320**	0.656**	0.619**	0.261**
ButterfliesS			1	0.425**	0.368**	0.011	0.547**	0.218**	0.098**	0.511**	0.522**	0.268**
GeomorphologyS				1	0.206**	-0.041	0.301**	0.159**	-0.174**	0.329**	0.272**	0.176**
SoilS					1	0.003	0.549**	0.142**	0.370**	0.615**	0.403**	0.197**
RockS						1	0.041	-0.013	-0.021	-0.053	-0.008	0.052
Carbon							1	0.222**	0.382**	0.698**	0.731**	0.183**
Groundwater								1	0.093**	0.220**	0.206**	0.100**
Milk&Meat									1	0.569**	0.175**	0.166**
Crop										1	0.457**	0.317**
Free-time res.											1	0.166**
Landscapes												1

In the VP, overall explained variation varied strongly among the six studied ESs, ranging from 3.5% for potential production of groundwater to 73.8% for forest carbon budget (Fig. 3). The independent effect of biodiversity was higher than that of geodiversity for forest carbon budget (27.2% and 5.3%, respectively), potential production of groundwater (4.9% and 1.2%), crop production (10.9% and -1.7%), amount of free-time residences (28.9% and 4.9%) and nationally valuable landscapes (6.3% and 1.7%). The shared fraction of biodiversity and geodiversity varied from 0.4% (groundwater) to 41.3% (forest carbon budget).

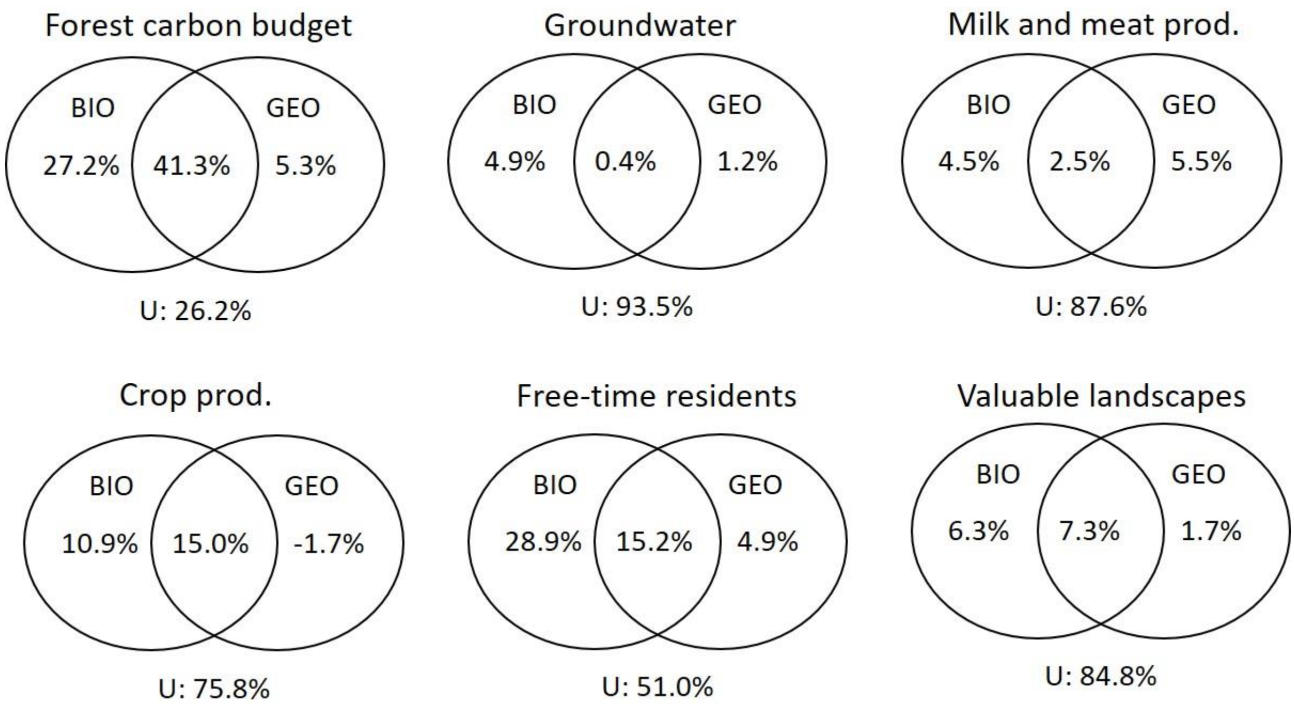

Fig.3. The relative roles of biodiversity (BIO) and geodiversity (GEO) in explaining six ecosystem services (i.e., forest carbon budget, potential production of groundwater, milk and meat production, crop production, amount of free-time residences and national valuable landscapes) using variation partitioning based on generalized linear models.

Forest carbon budget and the number of free-time residences were structured by vascular plants and nesting birds of biodiversity variables and geomorphological and soil richness of geodiversity variables (Table 3). Although the variation in the ground water data was poorly explained, a total of four variables were in the final VP models, namely vascular plants, nesting birds, geomorphological and rock richness. All the six biodiversity and geodiversity variables explained the meat and milk production, whereas all except the vascular plants variable were in the final crop production and national valuable landscapes models.

Table 3. The linear (L) and quadratic (Q) terms of the explanatory variables selected from biodiversity and geodiversity variable groups and used in the variation partitioning for modelling six ecosystem services. S associated with the biodiversity and geodiversity variables refers to the richness of a particular variable.

	PlantsS	BirdsS	ButterfliesS	GeomorphologyS	SoilS	RockS
Forest carbon budget	+−Q	+−Q		+−Q	+−Q	
Groundwater	+−Q	−+Q		+−Q		−L
Milk and meat production	+−Q	+L	+−Q	−+Q	−+Q	−L
Crop production		−+Q	−+Q	+−Q	−+Q	+−Q
Free-time residences	+−Q	+−Q		+−Q	+L	
Valuable landscapes		−+Q	+−Q	+L	−+Q	−+Q

3.2. Trade-offs between biodiversity and geodiversity and ESs

GAMs indicated that increase in biodiversity (i.e., total species richness) enhanced forest carbon budget (model's D^2 = 66.8%), potential production of groundwater (8.3%), crop production (35.7%), free-time residences (40.0%) and valuable landscapes (11.6%) (Fig 4). However, this positive trend levelled off for the first three ESs. For the milk and meat production (7.7%), the relationship with biodiversity was hump-shaped.

Geodiversity (i.e., total georichness) was positively related to forest carbon budget (model's D^2 = 12.4%), potential production of groundwater (0.1%), crop production (8.9%), free-time residences (7.9%) and valuable landscapes (6.9%) (Fig. 5). This pattern levelled off for forest carbon budget and crop production. A hump-shaped pattern was found between geodiversity and milk and meat production (0.9%).

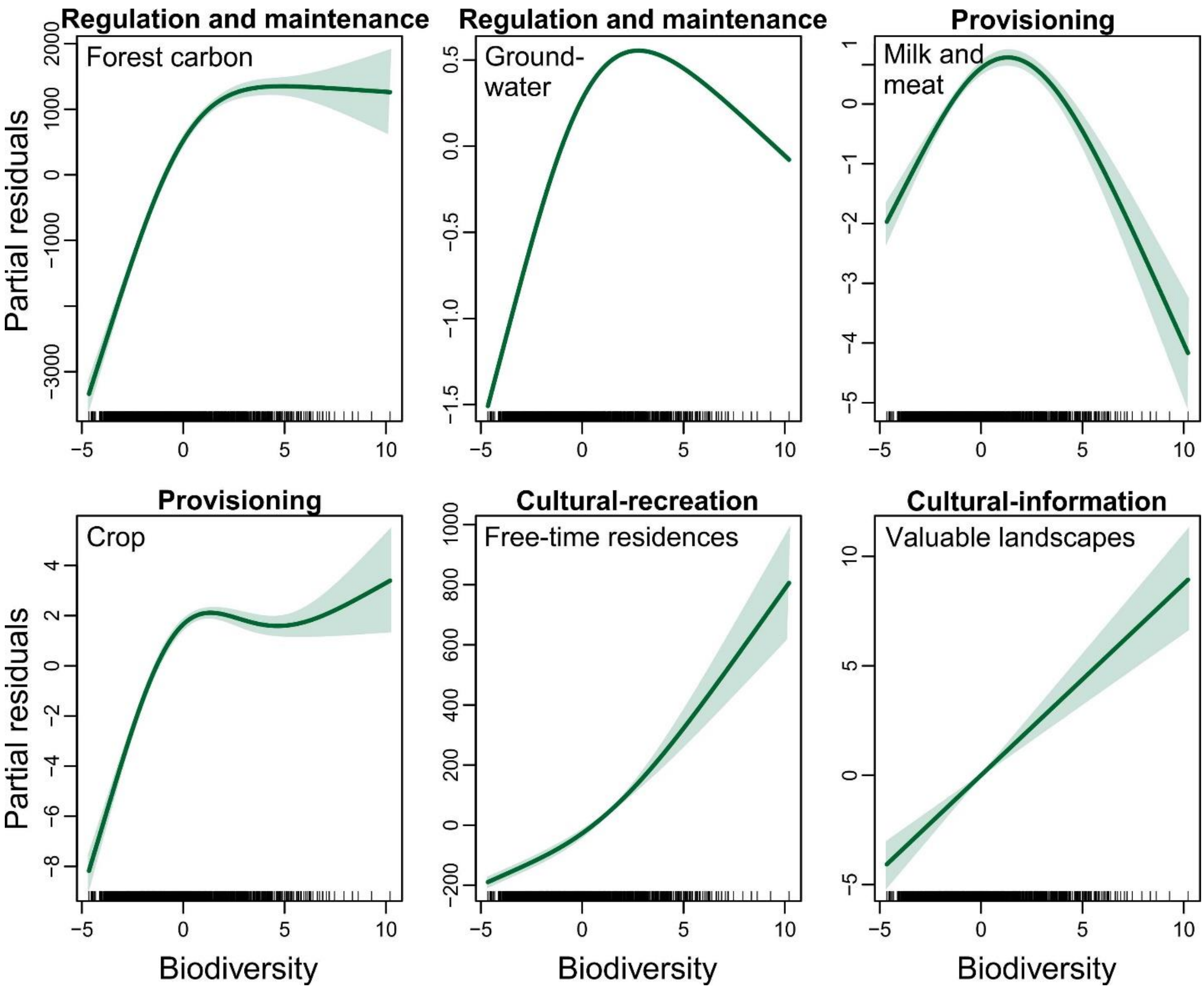

Fig. 4. Response curves with 95% confidence limits of biodiversity in relation to the forest carbon budget, the potential production of groundwater, milk and meat production, crop production, free-time residences, and valuable landscapes. The response curves were obtained through generalized additive models (GAMs) using univariate models [y-axis = partial residuals and estimated degrees of freedom of the smoother (s) function, x-axes = standardized values of explanatory variable i.e. total biodiversity].

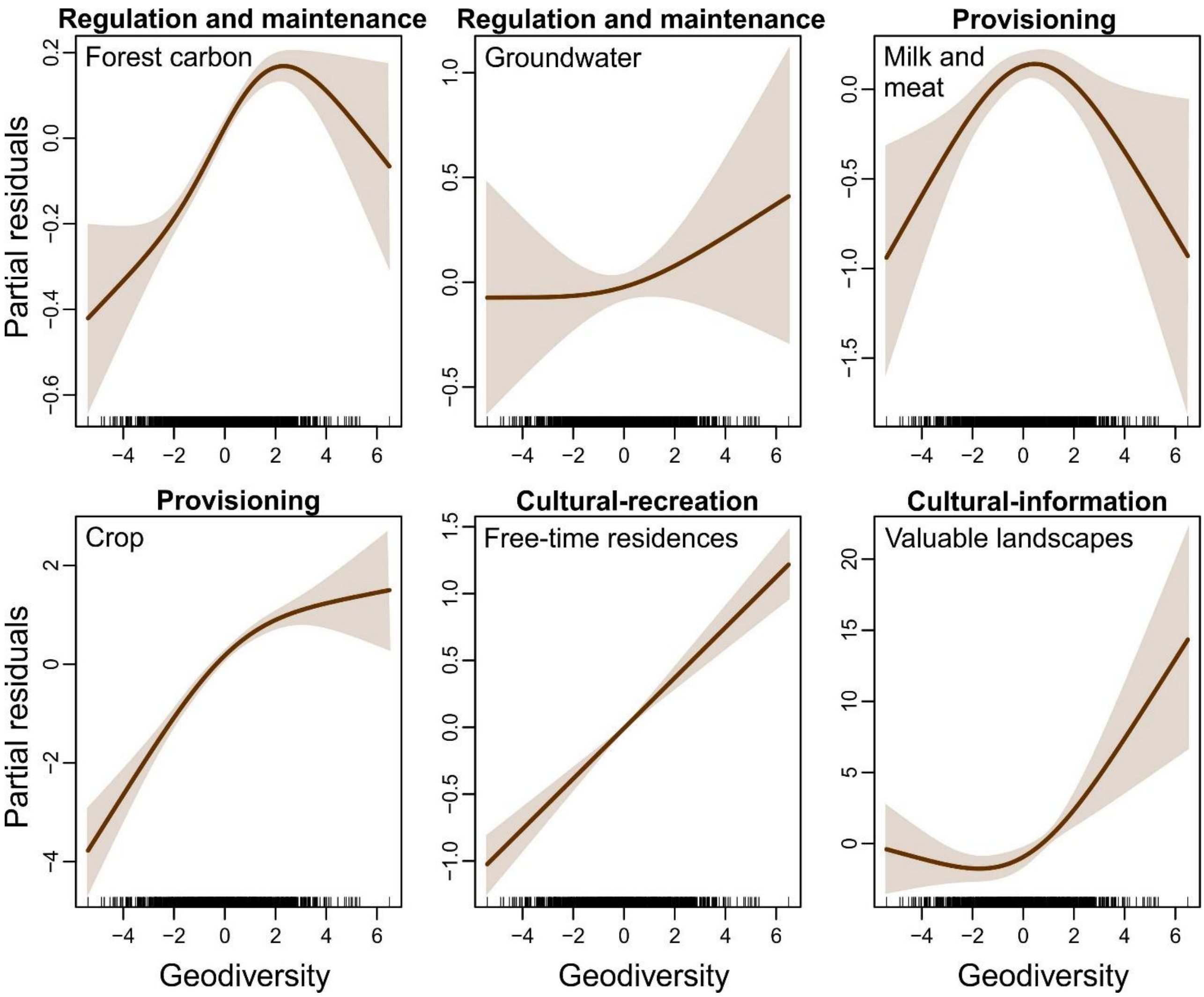

Fig. 5. Response curves with 95% confidence limits of geodiversity in relation to the forest carbon budget, the potential production of groundwater, milk and meat production, crop production, free-time residences, and valuable landscapes. The response curves were obtained through generalized additive models (GAMs) using univariate models [y-axis = partial residuals and estimated degrees of freedom of the smoother (s) function, x-axes = standardized values of explanatory variable i.e. total georichness].

4. DISCUSSION

There has been a growing interest to include abiotic diversity to ESs research (Gray 2012; Gordon and Barron 2013; van Ree and van Beukering 2016). We followed this approach by mapping geodiversity, biodiversity and six different ESs across 1006 grid cells of 100 km^2 covering the whole Finland to better understand whether there are spatial overlapping between different diversity patterns and ESs. We found that geodiversity was an important complementing factor in explaining spatial variation of the studied ESs. Although the independent contribution of geodiversity was low in the variation partitioning, the shared fraction of biodiversity and geodiversity was high, often exceeding that of both independent fractions. In addition, the response curves of GAMs demonstrated that higher geodiversity mainly increased ESs, resulting to synergic (win-win) effects between abiotic diversity and ESs. For forest carbon budget and the two provisioning services there occurred a threshold at higher geodiversity values after which the positive effect levelled off or turned to negative. To our knowledge, this is the first case study where geodiversity, including several abiotic features, has been related to ESs to study their spatial variation, in addition to quantify synergic and trade-off effects, at broad scales.

4.1. Biodiversity primarily explains but geodiversity complements spatial variation of ESs

The independent effect of biodiversity was higher than that of geodiversity in explaining spatial patterns of ESs in five cases out of six, with an exception of milk and meat production. This finding suggests that the link between biodiversity and different ESs is much stronger compared to geodiversity and ESs. The importance of biodiversity in regulating ecosystem processes, being a final ES or a good has been well-recognised in literature (Mace et al. 2009; Haines-Young and Potschin 2010). However, we also found a high shared effect of biodiversity and geodiversity in structuring ESs across Finland, indicating that these two facets of diversity are essentially interlinked and are both important in explaining spatial variation of ESs at the study scale (Gordon and Barron, 2012; van Ree and van Beukering, 2016). This is not surprising, because abiotic diversity can also interact with biodiversity with important consequences for ESs (Gray 2008; Gordon et al. 2012). For instance, different habitats originate from different geological attributes, landforms and processes. In addition, abiotic components of ecosystems affect micro-climates, facilitate nutrient cycling and create niche space for various species (Nichols et al. 1998; Matthews 2014; Lawler et al. 2015). Higher geodiversity also enables more niches within the same environment, allowing a higher degree of biodiversity to co-exist at broad scales (Parks and Mulligan 2010; Matthews 2014). Thus, geodiversity in the form of variable soil and rock types, in addition to different geomorphological landforms, enables existence of higher number of vascular plants and nesting birds (see Tukiainen et al. 2017b), which were the most important components of biodiversity in our study.

The shared effect of geodiversity and biodiversity had the strongest contribution to forest carbon budget, crop production, free-time residences and valuable landscapes. Carbon sequestration in forests is a result of biodiversity, which in turn is founded on geodiversity (Gray 2012; Gordon and Barron 2012). Thus, variety of different soils and geomorphological landforms has likely created a mosaic of habitats that enable efficient carbon binding in the Finnish boreal forests. For the crop production, agricultural activities are often situated in fertile river valleys in Finland, where also exists different soils types and geomorphological landforms. The high shared effect of geodiversity and biodiversity for the free-time residences and valuable landscapes is related to landscape heterogeneity. The free-time residences are situated close to fresh waters in Finland, and these areas show high environmental variation related to geomorphology. Different soil and rock features promote higher variation in geomorphological landforms (Hjort et al. 2012; Matthews 2014). Nationally valuable landscapes are found in diverse environments, ranging from peatlands and traditional agricultural landscapes to topographically variable tree-covered hills (Ala-Hulkko et al. 2016), that originate from variable number of abiotic features. As these valuable landscapes with different environments harbor different levels of habitats for species, the strong link between geodiversity and biodiversity is rather evident. Similarly, Gordon and Barron (2012) identified regarding valuable landscapes that the range of habitats explicitly corresponded to geodiversity in Scotland.

In addition to the environmental perspective, the inclusion of geodiversity to ESs research has an important methodological aspect. Investigation of environmental patterns has become more challenging due to the increasing complexity of study designs and ecosystems (Low-Decarie et al. 2014). They showed with an exhaustive review of more than 18 000 papers that explanatory power of ecological studies has decreased likely as a result of the increase in ecosystem complexity. Overall explained variation was improved for majority of ESs when geodiversity was included in our models. For example, geodiversity (together with independent and shared effects) accounted for 63% of overall explained variation for forest carbon budget, 64% of variation for milk and meat production, and 59% of variation for nationally valuable landscapes. This suggests that the consideration of geodiversity in ESs research has benefits beyond merely environmental perspective but it helps us to improve our model performance at broad scales.

4.2. Geodiversity and biodiversity promote ESs but for certain services only until a threshold

We assumed based on schematic generalizations (Fig. 1) that increasing diversity increases regulating services, whereas a hump-shaped pattern dominate between diversity and provisioning and cultural services. Our results only partly followed these hypotheses. As expected, there was a hump-shaped or positive but saturating relationship between both diversity measures and the two studied provisioning services. Similarly, biotic and abiotic diversity showed a clear positive pattern in relation to recreation services. However, we found no drop in the pattern between both diversity measures and cultural-recreation service in the high diversity areas suggested by our conceptual framework but the pattern was linearly positive. These findings suggest that synergic (win-win) effects were found between the diversity patterns and cultural services (i.e. diverse landscapes attract people). On the contrary, biodiversity and geodiversity first promoted forest carbon budget and potential production of groundwater but the pattern levelled off until a threshold value. Thus, synergic effects were evidenced for regulating and provisioning services until a threshold after which trade-off effects were dominant between the diversity patterns and these ESs. This means that trade-off effect may be the dominant relationship if biotic and abiotic diversity are at high to very high level. Although human pressures are currently relatively modest in Finland compared to many other regions, many studies have reported that land use and climate change already severely threaten diversity in the boreal and sub-Arctic regions (Hanski 2000; Sala et al. 2000; Vilmi et al. 2017).

One likely explanation for these unexpected patterns may be that the degree of both biodiversity and geodiversity is relatively small at the boreal environments (Tukiainen et al. 2017b), where high diversity values are mostly lacking. In addition, geographical scale of a study clearly affects how the natural diversity explains ESs (Anderson et al. 2009; Malinga et al. 2015; Burkhard and Maes 2017). In our work, the used broad study scale results to averaging of extreme diversity values. However, the relationship may be different at more finer spatial scales (e.g., resolution and/or extent), although geodiversity is typically most influential at regional scales, where variation among different abiotic features is the widest (Gray 2012; Hjort & Luoto 2012). These two issues (i.e., lack of high diversity and scale) probably explain our findings for those diversity and ESs patterns that differed from the a priori conceptual theory.

Increase in both geodiversity and biodiversity enhanced forest carbon budget until a certain threshold after which the positive association levelled off (biodiversity) or turned to negative (geodiversity). Thus, the relationship mainly followed the theory at low and moderate but not at high diversity values. The relationship between diversity and regulating services are often dependent on the service under investigation and generalizations over all regulating services are difficult to draw (de Groot et al.

2010; Science for Environment Policy 2015). Our findings indicate that there is a threshold how much forest can bind carbon with increasing landscape heterogeneity. The positive but eventually stabilising relationship between natural diversity and forest carbon budget suggests that there is a win-win situation at low and medium values but this changes to trade-off effect in high diversity values. High geodiversity is probably related to dynamic landscapes with high geomorphological process activity (Hjort and Luoto 2010; Gray 2013) that may reduce growth conditions and carbon binding capacity. Our findings contradict with the other studies, where areas of carbon supply were negative associated with biodiversity in the UK and French Alps (Anderson et al. 2009; Maskell et al. 2013).

Similar kind of threshold was discovered between natural diversity and crop productions, as geodiversity and biodiversity boosted crop production in the low and mean values but levelled off at the high diversity values. This was expectable, because extensive crop monocultures cannot exist in abiotically diverse environments and support low levels of biodiversity (e.g., Altieri 1999). Increasing diversity increased crop production until the natural high diversity regions which is inaccessible for human use. Provisioning services are considered to be non-existent or low for an ecosystem in its natural state with poor accessibility (de Groot et al. 2010). Similarly to our study, Anderson et al. (2009) and Maskell et al. (2013) reported a positive relationship between (plant) biodiversity and agricultural value at a country and regional extent, respectively. The patterns between natural diversity and the potential production of groundwater and milk and meat production followed rather well the theoretical expectations (Figs. 1, 4 and 5). However, owing to the low explanatory power of the models extensive conclusions of the relationships cannot be drawn.

Expectedly, biodiversity and geodiversity were positively related to free-time residences and valuable landscapes, indicating that there is a synergic effect between them. Several studies have reported that synergic effects are easier found between diversity and cultural services than other service categories (Howe et al. 2014; Cavender-Bares et al. 2015; Lee and Lautenbauch 2016). However, we did not find an evident decrease in cultural-recreation services in high diversity values illustrated in the theoretical framework. Accessibility to cultural-recreation services fundamentally determines their usability (de Groot et al. 2010). For example, Ala-Hulkko et al. (2016) found that it takes only ca. 100 minutes by car to reach their closest national park but ca. 700 minutes to drive to the nearest wilderness area for all Finns. It seems, however, that the studied cultural-recreation services are well-accessed even in high diversity areas situated mostly in Southern Finland. This highlights the importance of accessibility in explaining the relationship between overall diversity and cultural(-recreation) ES.

Although we found that the inclusion of geodiversity is worthwhile in the broad-scale ES research done in the boreal region, more research is needed to find support for our results in different spatial scales and regions. The importance of geodiversity for biodiversity and ESs is typically highest at the intermediate regional scales (e.g., Lawler et al. 2015) that may limit it's use at other scales (but see Bailey et al. 2016 for 1km resolution study and le Roux and Luoto 2014 for local plant community study). In addition, the found patterns may differ in more human disturbed environments. For example, Santos et al. (2017) recently discovered that urbanization impacted a significant portion of the areas classified with high geodiversity in Brazil. It should also be noted that the used ES were not actual final services according to CICES (2018), because we do not know how much of these ES are actually used or consumed by people (see discussion of classification in Boyd and Banzhaf 2007 and Fisher et al. 2009). However, information on the exact consumption was available for all studied ESs. Moreover, milk and meat production are strongly related to farms, not to nature *per se* as suggested by the ES concept (Millennium Ecosystem Assessment 2005). This resulted to the moderate explained variation between both diversity measures and milk and meat production. The potential production of groundwater was similarly poorly explained in our study.

5. Conclusions

Our empirical study lends support for previous synthesis, classifications and theoretical papers that geodiversity should be deeply integrated to ESs research (Gordon and Barron 2012; van Ree and van Beukering 2016; CICES 2018). Geodiversity is an essential part of ecosystem functioning and services (Matthews 2014; Hjort et al. 2015; Lawler et al. 2015), and together with biodiversity, they form foundations for numerous ESs in different ecosystems. Thus, neglecting of geodiversity in ESs research would severely make contemporary scientific efforts to understand the link between humans and the environment deficient. Fortunately, ESs research has woken up to realise the importance of geodiversity in structuring different services at various scales (e.g., van Ree and van Beukering 2016; CICES 2018). In addition, by interlinked with biodiversity through sustaining growing conditions for various species and maintaining ecological niche spaces, geodiversity is fundamentally related to the struggle against climate and land use changes (Anderson and Ferree 2010; Lawler et al. 2015). However, not only is biodiversity under threat of global change, but human actions also compromise the quality and quantity of geodiversity in the future (Gordon and Barron 2012). For example, urbanization and mineral resources extraction create a severe risk to the sustainable use of abiotic environment in the coming years (van Ree and van Beukering 2016; Santos et al. 2017; Tukiainen et al. 2017b). One must remember that many of the abiotic features have established during thousands and millions of years and once they are destroyed or used up, these features are virtually forever lost for the modern society (e.g., Gray 2013). Thus, both environmental conservation and management would benefit from the deeper integration of geodiversity into ESs research in the changing environmental conditions faced in the coming decades.

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