

# 1 **Is catchment geodiversity a useful surrogate of aquatic plant species** 2 **richness?**

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4 Maija Toivanen <sup>\*1</sup>, Jan Hjort<sup>1</sup>, Jani Heino<sup>2</sup>, Helena Tukiainen<sup>1</sup>, Jukka Aroviita<sup>2</sup> and Janne  
5 Alahuhta<sup>1,2</sup>

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7 1 University of Oulu, Geography Research Unit, P.O. Box 3000, 90014 University of Oulu, Finland

8 2 Finnish Environment Institute, Freshwater Centre, Paavo Havaksen Tie 3, FI-90570 Oulu, Finland

9 \*Corresponding author: maija.toivanen@oulu.fi

## 10 11 **ABSTRACT AND KEYWORDS**

12 **Aim** Conserving freshwater biodiversity in a rapidly changing world requires updated planning  
13 schemes and research efforts. Geodiversity – the diversity of Earth surface forms, materials and  
14 processes – and biodiversity are interlinked at a fundamental level. This relationship is being  
15 considered in a growing number of studies, yet research from freshwater environments is scarce.  
16 We used geodiversity (rock-type, soil-type and geomorphological richness), local and climatic  
17 variables to explore whether geodiversity can be used as a surrogate for aquatic plant species  
18 richness in lakes and rivers.

19  
20 **Location** Finland

21  
22 **Taxon** Aquatic plants

23  
24 **Methods** We compared geodiversity variables (measured within 1-km<sup>2</sup> grid cells) to well-studied  
25 local (e.g., area, alkalinity) and climate (e.g., growing degree-days) variables, and examined the  
26 patterns between habitat types (lakes and rivers) and among all taxa and major functional groups  
27 (helophytes and hydrophytes). We modeled lake (n=145) and river (n=146) plant species richness  
28 with generalized linear models, and further partitioned variation to measure the independent and  
29 shared contributions of the geodiversity, climate and local environmental variable groups. As a  
30 complementary analysis, and to identify single important variables explaining variation in aquatic  
31 plant species richness, we utilized boosted regression trees.

32  
33 **Results** We found a positive relationship between aquatic plant species richness and catchment  
34 geodiversity variation with recurring patterns across two different freshwater habitat types and two  
35 aquatic plant functional groups. Higher variation in geodiversity (measured at landscape scale)  
36 supported higher freshwater biodiversity (measured at the local scale) of lakes and rivers.

37  
38 **Main conclusions** Geodiversity can be a useful addition to biodiversity modeling, and it should be  
39 considered in conservation schemes and monitoring efforts, further supporting the principle of  
40 conserving nature's stage. Yet, differences between habitats and functional groups suggest that  
41 more habitat-specific approaches and multiple biodiversity measures should be considered. Our  
42 study is an important signpost guiding further studies on the biodiversity-geodiversity relationship  
43 in freshwater ecosystems.

44  
45 **Keywords:** abiotic surrogates, biodiversity, conserving nature's stage, functional groups,  
46 geodiversity, lakes, macrophytes, rivers

# 1 INTRODUCTION

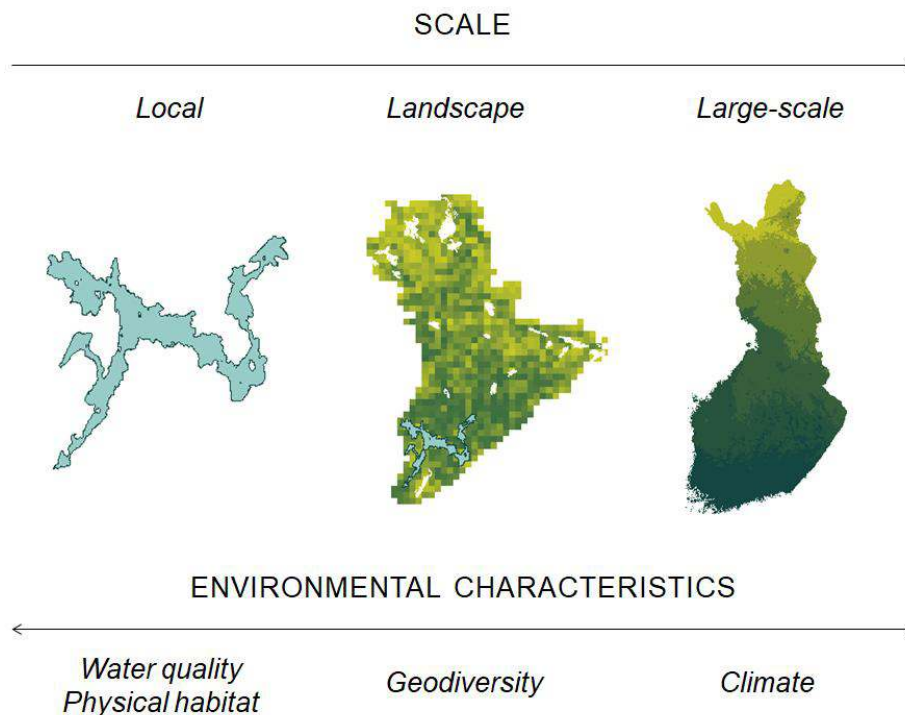
2 A growing need to conserve and manage biodiversity in the rapidly changing world (Sala *et al.*,  
3 2000; Dudgeon *et al.*, 2006; Vilmi *et al.*, 2017) requires updated planning schemes and efforts.  
4 Inclusion of abiotic surrogates of biodiversity has a high potential to improve the efficiency of  
5 conservation planning (Parks & Mulligan 2010; Tukiainen *et al.*, 2017a) offering a more holistic  
6 understanding of interactions between biotic and abiotic environments (Antonelli *et al.*, 2018).  
7 Geodiversity – the diversity of Earth surface forms, materials, and processes (Gray, 2013) –  
8 presents abiotic (or physical) diversity and is related to biodiversity at a fundamental level as well  
9 as in a growing number of studies. However, the idea of interlinked ecosystems and the connection  
10 between spatially-structured biological, physical and further cultural properties was already  
11 acknowledged by Alexander von Humboldt, a pioneer of modern biogeography (1769–1859). Due  
12 to Humboldt’s extensive work on vegetation zone mapping and modern studies linking biotic and  
13 abiotic environments, our knowledge on the importance of geodiversity for living things and their  
14 adaptation to environmental changes has grown considerably (Anderson & Ferree 2010; Hjort *et al.*,  
15 2015; Antonelli *et al.*, 2018).

16  
17 Despite the strong historical background, research on the biodiversity-geodiversity relationship is in  
18 its infancy. Yet, it has a practical background in modern conservation biology. Lawler *et al.* (2015)  
19 stated that, under global change, protecting diversity of abiotic conditions would likely best  
20 conserve biodiversity in the future. This viewpoint can be considered through ‘Conserving Nature’s  
21 Stage’ approach (CNS, Beier *et al.*, 2015; Lawler *et al.*, 2015), which centers on the notion that  
22 conserving abiotic (geo-)diversity is necessary for conserving biotic (bio-)diversity (e.g., Anderson  
23 *et al.*, 2015) and further ecosystem services (e.g., Hjort *et al.*, 2015; Alahuhta *et al.*, 2018). CNS  
24 regards geodiversity as the stage for biodiversity, hence creating an evident link between  
25 biodiversity and geodiversity.

26  
27 To utilize geodiversity sufficiently as a tool for decision making and conservation planning, more  
28 focused assessments of geodiversity and its relationship with biodiversity are needed (Parks &  
29 Mulligan, 2010). In practice, geodiversity data are in many cases easier and less expensive to obtain  
30 than biodiversity data (Hjort *et al.*, 2012), and the increasing availability of global datasets (e.g.,  
31 Hengl *et al.*, 2017) and various statistical methods (e.g., Bailey *et al.*, 2018) is making geodiversity  
32 mapping possible at different spatial scales. Many studies have recently found that explicit  
33 measures of geodiversity can add explanatory power to statistical models accounting for variation in  
34 biodiversity (Hjort *et al.*, 2012; Tukiainen *et al.*, 2017a; Bailey *et al.*, 2018) highlighting the  
35 importance of understanding the interactions between biodiversity and Earth-surface processes  
36 (Antonelli *et al.*, 2018). However, the existing body of research does not yet cover freshwater  
37 environments.

38  
39 Studies directly linking biodiversity and geodiversity are virtually lacking from freshwaters (but see  
40 Kärnä *et al.*, 2018 where local scale in-stream geodiversity measures were applied to explain  
41 variation in macroinvertebrate diversity), hindering our possibilities to understand whether  
42 geodiversity can be used as a surrogate for biodiversity in the freshwater realm. This deficiency is  
43 further emphasized by the fact that, in areas with numerous water bodies, it is challenging to  
44 measure direct abiotic characteristics (e.g., water chemistry and local physical habitat) for all water  
45 bodies. These characteristics can further vary strongly even between geographically close  
46 freshwater systems (Heino *et al.*, 2013; Heino & Tolonen, 2017).

47  
48 Freshwater ecosystems are shaped by multiple environmental factors operating at various spatial  
49 scales, such as water quality at local scale and climate at large-scale (Fig. 1; Lacoul & Freedman,  
50 2006; Alahuhta *et al.*, 2019). This highlights the importance to consider multi-scale variables



**Figure 1** Conceptual visualization of the environmental factors operating at different spatial scales (from lake-level to catchment area-scale and regional scales) relevant to freshwater ecosystems and biota. Geodiversity can be considered to operate most strongly at landscape scale (catchment area in our study; e.g., Bailey *et al.*, 2017), whereas local environmental variables contribute most strongly at lake level and climate variables contribute most strongly at regional scales (e.g., Lacoul & Freedman 2006; Alahuhta *et al.*, 2019). The visualized geodiversity variable is geomorphological richness and the climate variable is growing degree-days across Finland.

1 affecting these ecosystems (Soininen *et al.*, 2015). Catchment (i.e., landscape scale) approach  
 2 acknowledges the link between aquatic and terrestrial ecosystems, enabling a more comprehensive  
 3 view on biological communities and ecosystem functions than using local-scale (within-lake or  
 4 within-river) factors alone (Soininen *et al.*, 2015). It takes a step towards a more process-based  
 5 approach, recognizing the importance of conserving ecosystem processes instead of individual  
 6 species or habitats. Catchment properties, such as land cover, topography and geological qualities,  
 7 have been extensively used to explain water quality and biodiversity in freshwaters (Dodson *et al.*,  
 8 2005; Soininen & Luoto 2012; Domisch *et al.*, 2016). In contrast, geodiversity represents a more  
 9 complete characterization of Earth-surface heterogeneity compared with coarse topographic  
 10 variables. As topographic variables may oversimplify the physical environment, geodiversity, in its  
 11 broadest sense, includes aspects of geology, geomorphology, topography, hydrology and climate  
 12 (Parks & Mulligan, 2010). Such abiotic heterogeneity relates to extended local-resource gradients,  
 13 niche space, and habitat variety (Stein *et al.*, 2014; Matthews 2014). It offers an insight into  
 14 catchment area heterogeneity which can help reveal factors controlling biodiversity patterns beyond  
 15 climate and topographic variables.

16  
 17 In this study, we used three explicit geodiversity variables (soil-type richness, rock-type richness  
 18 and geomorphological richness) that have been developed and studied rather extensively in  
 19 terrestrial landscapes (Hjort & Luoto 2010; Hjort *et al.*, 2012; Tukiainen *et al.*, 2017a) in relation to  
 20 human impact (Tukiainen *et al.*, 2017b; Räsänen *et al.*, 2017) and scale-related influences (Bailey *et*

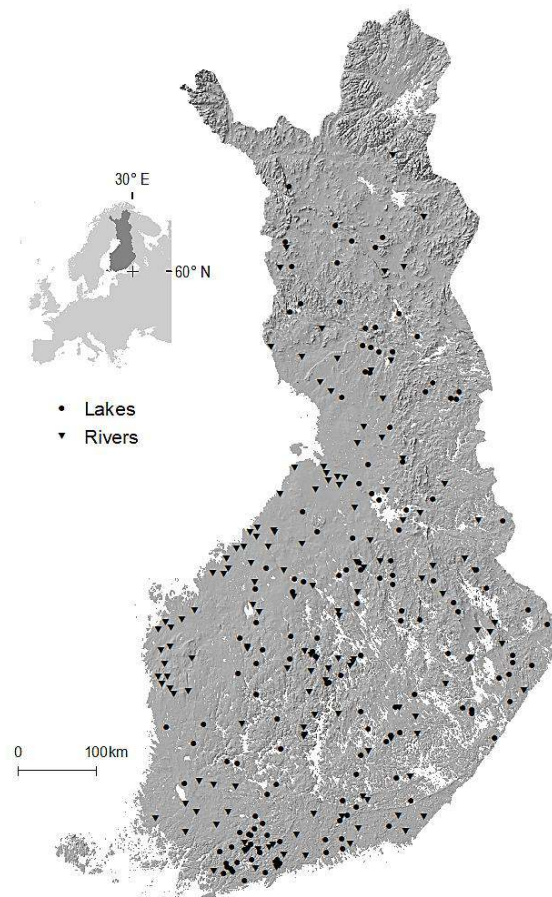
1 *al.*, 2017). Our overall aim was to investigate whether geodiversity could act as a surrogate for  
2 aquatic plant species richness in two different freshwater habitats (i.e., lakes and rivers). More  
3 precisely, we studied: (1) how does a set of three environmental variables (local, geodiversity,  
4 climate) explain patterns in species richness of aquatic plants, (2) do the detected patterns in aquatic  
5 plant species richness vary between the lakes and rivers, and (3) do different functional plant groups  
6 (i.e., helophytes vs. hydrophytes) respond differently to local, geodiversity and climate variables?  
7

8 To disentangle the first study question, we focused on a variety of local and climate variables that  
9 are known to affect aquatic plant species richness (Toivonen & Huttunen, 1995; Vestergaard &  
10 Sand-Jensen, 2000; Akasaka & Takamura, 2011; Alahuhta, 2015), in addition to geodiversity  
11 variables that represent a novel aspect in modeling freshwater biodiversity. First (H<sub>1</sub>), we  
12 hypothesized that catchment geodiversity brings added value to modeling aquatic plant richness  
13 based on outcomes derived from terrestrial plants (Tukiainen *et al.*, 2017a; Tukiainen *et al.*, 2017b;  
14 Bailey *et al.*, 2018). However, we expected local variables to contribute most strongly to aquatic  
15 plant species richness, because water quality and physical habitat conditions are often key  
16 environmental factors structuring aquatic plant communities (Vestergaard & Sand-Jensen, 2000;  
17 Viana, *et al.*, 2014; Alahuhta 2015). Second (H<sub>2</sub>), we expected catchment geodiversity to have a  
18 similar influence on aquatic plant species richness in lakes and rivers, because catchment geological  
19 and geomorphological qualities similarly provide a base for the key habitat factors influencing  
20 aquatic plants (e.g., water chemistry and land cover; Lacoul & Freedman, 2006). Third (H<sub>3</sub>), we  
21 assumed to find differences between functional groups in their response to environmental variables,  
22 because helophytes and hydrophytes differ in their accessibility to carbon and nutrient storages, and  
23 may thus show different responses to water quality and hydromorphological variables (Toivonen &  
24 Huttunen, 1995; Akasaka *et al.*, 2010; Alahuhta *et al.*, 2014; Kolada, 2016).

## 26 **2 MATERIALS AND METHODS**

### 27 **2.1 Aquatic plant data**

28 In this study, we used aquatic plant data from 145 lakes and 146 rivers across Finland (Fig. 2). The  
29 recorded aquatic plants included both hydrophytes (or true aquatic plants) and helophytes (or  
30 emergent species and shore plants). Lake data were collected between 2006–2012 and river data  
31 between 2009–2012 and maintained by Finnish Environment Institute (SYKE). Total species  
32 richness varied between 13–55 (helophytes 3–30, hydrophytes 2–31) in lakes, and between 1–26  
33 (helophytes 1–20, hydrophytes 1–12) in rivers. Full species list and functional groups are presented  
34 in Appendix S1 (Tables S1.1–S1.2 in Supporting Information).



**Figure 2** Sampled lakes (n=145) and river reaches (n=146). The grey background is a hillshade image visualizing topography of Finland (National Land Survey of Finland). Lakes on the map are shown in white.

1  
 2 Lake plants were surveyed using a main belt transect method (Leka *et al.*, 2003). Transects are five-  
 3 meter-wide sections positioned perpendicularly to the shoreline. Each transect extends from the  
 4 upper eulittoral to the outer depth limit of vegetation, or to the deepest point of the basin if  
 5 vegetation covers the entire lake. Transects were divided into zones according to the dominant life  
 6 form or dominant species, and frequency and cover of each species were recorded. Plants were  
 7 observed by wading or by boat, with the aid of rake and hydroscope. River plants were sampled  
 8 using national version of the methodology based on international standard SFS-EN 14184  
 9 (Rääpysjärvi *et al.*, 2016). At each study reach, two 100-m sections, a riffle section and a pool  
 10 section, were surveyed. Each 100-m section was divided into five 20-m-long subsections, where  
 11 abundance and frequency of each vascular plant species were estimated. River plants were observed  
 12 by wading with the aid of rake. Due to the different plant survey methods, lake and river data sets  
 13 could not be pooled together, and we therefore studied lake and river plants separately. We used  
 14 presence-absence data of lake and river plant species in the statistical analysis.

15  
 16 **2.2 Environmental data**

17 We used three sets of environmental variables as predictors of aquatic plant species richness: (i)  
 18 local, (ii) catchment geodiversity and (iii) climate variables. Descriptive statistics are presented in  
 19 Appendix S1 (Table S1.3).

20

1 Local variables included alkalinity (mmol/L), total phosphorus (TP,  $\mu\text{g/l}$ ), water colour (mg Pt  $\text{l}^{-1}$ )  
2 and area (for lakes,  $\text{km}^2$ ) or width (for rivers, m). Alkalinity, TP and colour represented mean values  
3 of multiple samples during growing season between 2006 and 2012 for lakes and 2009 and 2012 for  
4 rivers. Lake surface area was delineated from geographic information system (GIS) data and river  
5 channel width was measured simultaneously with the plant surveys.

6  
7 We used the same environmental variables between lakes and rivers to enable comparison of results  
8 between these different habitat types. However, we used surface area for lakes and channel width  
9 for rivers, which both indicate habitat size for aquatic plants. Lake area is often used to represent  
10 the species-area relationship for aquatic organisms (Jones *et al.*, 2003). It can be problematic as  
11 large extent of a lake might be too deep for aquatic plant colonization and growth (Vestergaard &  
12 Sand-Jensen, 2000). However, in our data, maximum colonization depth was not available.  
13 Shoreline length reflects relatively well species-area relationship for aquatic organisms  
14 (Søndergaard *et al.*, 2005). We thus correlated lake area with shoreline length ( $r=0.935$ ,  $p<0.001$ )  
15 delineated from GIS to validate using lake area as proxy for habitat size.

16  
17 Geodiversity variables (mean and standard deviation of soil-type richness, rock-type richness and  
18 geomorphological richness) were calculated for catchment areas with zonal statistics tools in  
19 ArcMap 10.3. They were measured as the number of features (i.e. soil types, rock types or landform  
20 features) within each catchment area in  $1\text{-km}^2$  grid cell. Soil and rock types were derived from  
21 digital soil and bedrock maps, respectively, produced by the Geological Survey of Finland (GSF,  
22 2010a, b). Classifications of soil and rock types are listed in Appendix S1 (Table S1.4). Modeling  
23 of geomorphological richness for Finland is presented in detail in Tukiainen *et al.* (2017a).  
24 Geomorphological features included process units and landforms from different geomorphological  
25 process groups (aeolian, biogenic, cryogenic, fluvial, glacial, glaciofluvial, littoral and marine,  
26 polygenetic bedrock, slope and mass-wasting and weathering).

27  
28 Climate data for 1981–2010, at  $1\text{-km}^2$  resolution for catchment areas, were derived from the Finnish  
29 Meteorological Institute (FMI, Pirinen *et al.*, 2012). Climate variables considered were mean  
30 temperature of the coldest month (January), annual temperature sum above  $5^\circ\text{C}$  (growing degree-  
31 days, GDD) and mean annual precipitation. Increasing air temperature has a positive relationship  
32 with water temperature in boreal and temperate lakes, although lake characteristics can strongly  
33 mediate climatic effects, and spatial heterogeneity among lakes is typically large (Alahuhta, 2015;  
34 O'Reilly *et al.*, 2015).

35  
36 Prior to further data analysis, we explored Spearman correlations ( $R_s$ ) between pairs of predictor  
37 variables to avoid multicollinearity at the level of  $R_s > 0.7$ , following Dormann *et al.* (2013). Final  
38 variables were selected based on bivariate correlations and conceptual relevance (correlations  
39 presented in Tables S2.5–S2.6 in Appendix S2). For geodiversity variables, we considered both  
40 mean and standard deviation values, because catchment areas vary in size among lakes and rivers.  
41 Altogether, final data analysis included alkalinity, lake area (lakes), channel width (rivers), colour,  
42 total phosphorous (TP), standard deviation of soil richness (SoilStd), standard deviation of rock  
43 richness (RockStd) and standard deviation of geomorphological richness (GMStd).

### 44 45 **2.3 Statistical methods**

46 We generated generalized linear models (GLMs) for the richness of all taxa, helophytes and  
47 hydrophytes to identify important predictor variables separately for lakes and rivers using the  
48 “dredge” function in the R (R Development Core Team 2008) package ‘MuMIn’ (Barton, 2017).  
49 We used Gaussian or Poisson error distribution (with log link function) in the model fitting, and  
50 calculated adjusted explained deviance (adj.  $D^2$ ) values for each model with R package ‘modEvA’

1 (Barbosa *et al.*, 2016). Poisson error distribution was used with river hydrophyte richness and  
2 Gaussian error distribution with all other response variables. Models were ranked by corrected  
3 Akaike information criterion (AICc) values with a cut-off level of  $\Delta < 2$ . AICc is corrected for small  
4 sample size and considers sample size by increasing the relative penalty for model complexity with  
5 small data sets. Models with AICc differing by  $< 2$  are typically considered to have similar statistical  
6 support. This analysis also produces Akaike weights, which reflect the relative support for each  
7 model within AICc ranked models scaled to 0–1 (least to highest) (Burnham & Anderson, 2004).  
8 Sum of weights of ranked models ( $\Delta < 2$ ) is 1. From here, we refer to best models as the ones with  
9 the lowest delta value and largest weight value among the ranked models.

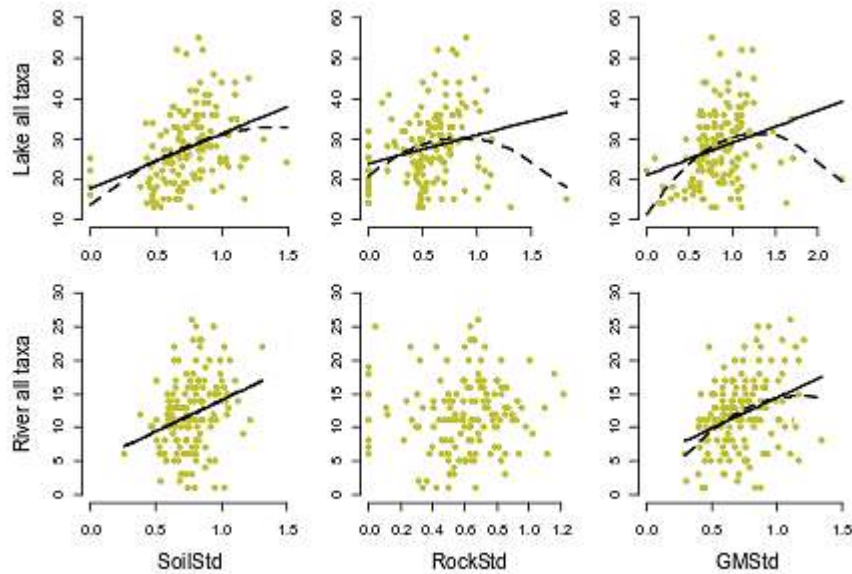
10  
11 To evaluate the spatial autocorrelation in our models, we calculated Moran's coefficients and  
12 correlograms based on lake geographical coordinates and residuals of the best GLMs (for each of  
13 the six response variables, respectively). Calculations were run with R package 'pgirmess' using the  
14 function "correlog" (Giraudoux, 2017).

15  
16 We used variation partitioning (VP, Legendre and Legendre 2012) following the approach of  
17 Hawkins *et al.*, (2003) to measure the independent and shared contributions of the local,  
18 geodiversity and climate environmental variable groups in explaining variation in aquatic plant  
19 richness in lakes and rivers. Consequently, we formed seven GLMs using (i) local, (ii) geodiversity,  
20 (iii) climate, (iv) local and geodiversity, (v) local and climate, (vi) geodiversity and climate  
21 variables and (vii) all variables from all three groups. Based on adjusted  $D^2$  values extracted from  
22 these seven separate GLMs, we calculated the independent and shared fractions for the three  
23 explanatory variable groups. Adjusted  $D^2$  values account for different number or environmental  
24 variables in different variable groups (Guisan & Zimmermann, 2000). We used both linear and  
25 quadratic terms of the explanatory variables to capture the potential nonlinear responses.

26  
27 To complement the GLMs, we analyzed the data with boosted regression trees (BRTs) (Elith *et al.*,  
28 2008) to estimate the relative influence of predictor variables on each response variable. We  
29 calibrated models with R package 'gbm' (Ridgeway, 2017) using function "gbm.step", which uses  
30 regularization methods to discourage overfitting and balance predictive performance with model fit  
31 (Hastie *et al.*, 2001). However, our interest was not in the predictive performance power but to  
32 recognize single important variables explaining aquatic plant species richness by taking the  
33 advantage of BRT's ability to recognize non-linear relationships without needing to transform data  
34 or eliminate outliers prior to the data analysis (Elith *et al.*, 2008). Following the rules of thumb  
35 discussed in Elith *et al.* (2008), we used a tree complexity of 4, learning rate of 0.001 and bag  
36 fraction of 0.5. Poisson error distribution was used with river hydrophyte richness variable and  
37 Gaussian error distribution with all other response variables.

### 38 39 **3 RESULTS**

40 First, we explored the relationship between species richness and geodiversity variables with  
41 scatterplots (Fig. 3).



**Figure 3** Scatterplots of species richness of aquatic plants in Finland and geodiversity (standard deviation values) variables. Regression lines are (solid for linear, dashed for quadratic terms) fitted if statistically significant ( $p < 0.001$ ). Scatterplots of local and climate variables are presented in Appendix S3 (Fig. S3.2). See Section 2.2 for abbreviations.

1

### 2 **3.1 Generalized linear models**

3 The amount of deviance (adjusted  $D^2$ ) explained in the AICc ranked GLMs are presented in Table  
 4 1. Full statistic details of the models are presented in Tables S3.7–S3.8 in Appendix S3.

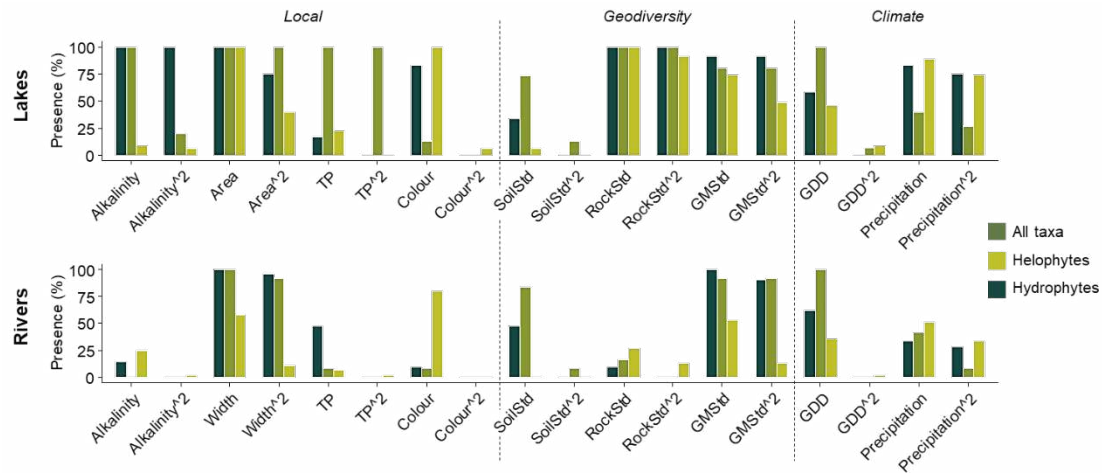
**Table 1** Adjusted  $D^2$  values for generalized linear models explaining aquatic plant species richness in Finland across all ranked models with AICc values  $< 2$ .

	Lakes	Rivers
All taxa richness	0.411–0.430	0.179–0.209
Helophyte richness	0.576–0.596	0.244–0.272
Hydrophyte richness	0.409–0.439	0.152–0.194

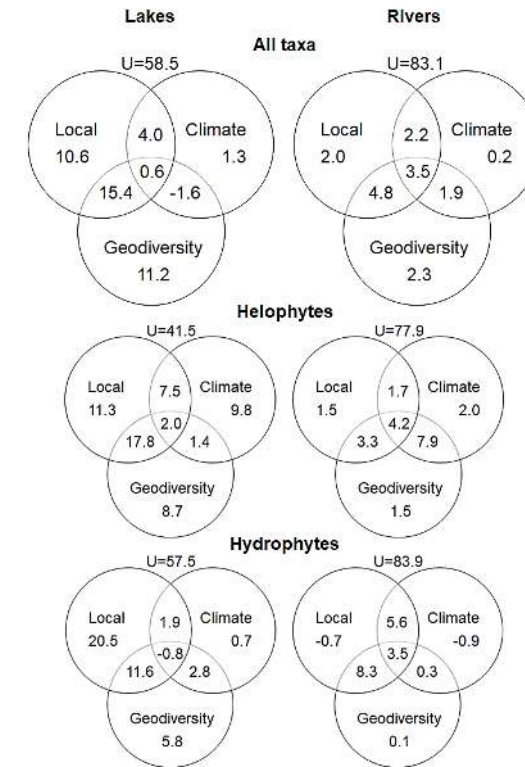
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6 Variable presence (%) in GLMs is presented in Figure 4. For lake species richness, area and  
 7 RockStd were selected in every GLM despite the functional group. Additional always-selected  
 8 variables included alkalinity (for all taxa), alkalinity, TP and GDD (for helophytes) and colour (for  
 9 hydrophytes). In the case of models that explain river species richness, variables present in every  
 10 ranked model were width and GMStd (for all taxa), and width and GDD (for helophytes). For river  
 11 hydrophyte species richness, color was most often present (in 80% of models). Altogether, there  
 12 was more variation in the selected environmental variables in the models that explained river  
 13 species richness. Always-selected geodiversity variables RockStd and GMStd were positively  
 14 correlated with lake ( $r = 0.387$ ,  $p < 0.001$ ) and river ( $r = 0.276$ ,  $p < 0.01$ ) catchment area size,  
 15 respectively (Appendix S2, Tables S2.5–S2.6).

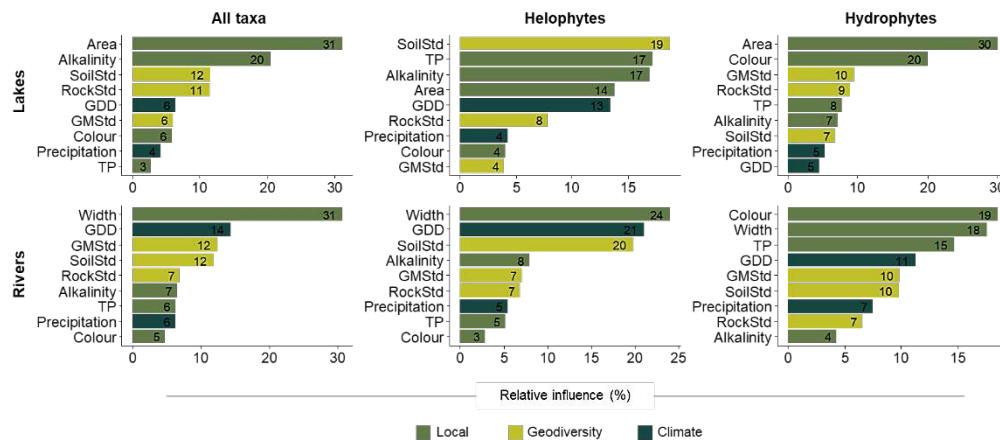




**Figure 4** Variables (linear and quadratic ( $\wedge^2$ ) terms) present in GLMs explaining lake species richness (out of 12, 15, 35 models for all taxa, helophyte and hydrophyte species richness, respectively) and river species richness (out of 21, 12, 45 models for all taxa, helophyte and hydrophyte species richness, respectively) of aquatic plants in Finland. Low values partly result from higher number of models generated. See Section 2.2 for abbreviations.



**Figure 5** Results of the variation partitioning, in terms of proportions of deviance accounted for (%) in aquatic plant richness in Finland into the independent contributions (geodiversity, local, and climate), the shared contributions and the undetermined variation (U). The negative shared variation can result from suppressor variables or two strongly correlated predictors with strong effects on the response of opposite signs (Legendre & Legendre 2012). Geodiversity variables were SoilStd, RockStd, GMStd. Local variables were alkalinity, color, TP, area (for lakes) and width (for rivers). Climate variables were GDD and precipitation. See Section 2.2 for abbreviations.



**Figure 6** The relative influence (%) of individual variables from the boosted regression tree analysis. Exact values for each variable are given inside the bars. All taxa, helophytes and hydrophytes refer to aquatic plant species richness in Finland. See Section 2.2 for abbreviations.

1 We checked the residuals of the best models for spatial autocorrelation (Fig. S3.1 in Appendix S3).  
2 In four models (lake hydrophyte, river all taxa, river helophyte and river hydrophyte species  
3 richness), there were statistically significant ( $p < 0.05$ ) spatial autocorrelations detected with low  $p$ -  
4 values and within various distances, suggesting no serious bias by spatial autocorrelation (see  
5 Hawkins *et al.*, 2007). Spatial patterns in our dataset closely reflected the inherent latitudinal  
6 climate gradient extending across study area

### 7 8 **3.2 Variation partitioning**

9 In the GLM-based VP (Fig. 5), either local or geodiversity variable group had the highest  
10 explanatory power in each dataset when looking solely at their independent contributions.  
11 Relatively, climate variable group contributed mostly to helophyte species richness both in lake and  
12 river datasets. Highest shared contribution was between local and geodiversity variable groups,  
13 except for river helophyte species richness, where the highest shared contribution was the one  
14 between geodiversity and climate variable groups. Undetermined variation varied between 40.3–  
15 56.8% in lakes and 76.5–83.5% in rivers.

### 16 17 **3.3 Boosted regression trees**

18 Lake area and river width had high relative influence (RI, %) on species richness variables in both  
19 habitats (Fig. 6). Noteworthy is that there were variables with clearly higher RI (e.g., RI of width  
20 for river all taxa richness) for many response variables compared to second highest RI. For some  
21 models (e.g., lake helophytes and river hydrophytes), the RI values of different environmental  
22 variables were distributed more evenly. The importance of individual variables from different  
23 variable groups varied between the response variables.

## 24 25 **4 DISCUSSION**

26 In this study, we found a positive relationship between aquatic plant species richness and catchment  
27 geodiversity variation (within 1-km<sup>2</sup> grid cells) with recurring patterns across habitats (i.e. lakes and  
28 rivers) and functional groups (i.e. helophytes and hydrophytes). Although local water quality and  
29 physical habitat variables (e.g., alkalinity, lake surface area, river channel width) were the most  
30 important ones in explaining variation in aquatic plant species richness, geodiversity variables  
31 (SoilStd, RockStd, GMStd) contributed significantly to the variation in aquatic biodiversity across  
32 habitats and functional groups. This supports our hypotheses and strengthens the ideas of previous  
33 terrestrial research that geodiversity contributes to biodiversity modeling and is a potential surrogate  
34 of freshwater biodiversity at catchment scale.

### 35 36 **4.1. Linking geodiversity to aquatic plant species richness**

37 First, we wanted to find out how well local, climate and geodiversity variables explain variation in  
38 species richness of aquatic plants. We found support for our first hypothesis ( $H_1$ ) as geodiversity  
39 variables brought added value to the modeling of aquatic plant richness. For instance, geodiversity  
40 variable group had the largest independent contribution to species richness of all taxa in both lakes  
41 and rivers (Fig. 5). Also, local variables contributed rather strongly to aquatic plant richness, as  
42 expected. Both habitat size (lake surface area and river channel width) and water quality (alkalinity,  
43 colour and TP) variables explained species richness relatively well, but the best models were  
44 achieved when geodiversity variables were present together with local and/or climate variables.

45  
46 Our results are generally in line with previous studies with similar geodiversity variables from the  
47 terrestrial realm (Hjort *et al.*, 2012; Tukiainen *et al.*, 2017a; Räsänen *et al.*, 2017; Bailey *et al.*,  
48 2018). In the recent study by Kärnä *et al.* (2018), local-scale in-stream geodiversity variables were  
49 found to complement traditional physical habitat and water quality variables in accounting for  
50 macroinvertebrate diversity. The methods and taxonomic group in the study by Kärnä *et al.* (2018)

1 were vastly different from ours in quantifying in-stream geodiversity. However, the results align  
2 with our catchment-scale approach, suggesting that both landscape and local scale geodiversity are  
3 important for freshwater biodiversity. Furthermore, similar results have now been presented for  
4 aquatic plants (our study), terrestrial vascular plants (e.g., Tukiainen *et al.* 2017a, Bailey *et al.*  
5 2017) and stream macroinvertebrates (Kärnä *et al.*, 2018). Correspondingly, Antonelli *et al.* (2018)  
6 found soil heterogeneity and topographic relief to be strong predictors of various taxa in mountains  
7 both at global and regional scales.

8  
9 Throughout the study, aquatic plant richness and geodiversity mostly showed a positive  
10 relationship, with some indications of negative hump-shaped responses (Fig. 3). In particular, we  
11 applied standard deviation values of geodiversity that represent the variation in geodiversity across  
12 catchment areas. This, in turn, is related to abiotic environmental heterogeneity. Both positive and  
13 unimodal responses have been observed in earlier research on the relationship between species  
14 richness and environmental heterogeneity (Stein *et al.*, 2014). However, environmental  
15 heterogeneity often scales positively with area, thus making it difficult to detect the individual  
16 effects of environmental heterogeneity and area (see Stein *et al.*, 2014). We studied catchment areas  
17 with varying size (Table S1.3 in Appendix S1), but calculated mean and standard deviation values  
18 from gridded geodiversity data to account for the well-known area effect. In our data, geodiversity  
19 (std values) were positively correlated with catchment area size, yet correlation was rather weak  
20 ( $r=0.115-0.384$ , Tables S2.4-2.5 in Appendix S2), suggesting that different size catchments should  
21 be studied separately. Naturally, larger catchments potentially hold higher geodiversity. However,  
22 catchment processes are an integral part of freshwater biodiversity and water quality (Dodson *et al.*,  
23 2005; Soininen & Luoto 2012; Soininen *et al.*, 2015) through interaction with local scale processes.  
24 Complementarily, we explored the relationship between local (within shoreline) geodiversity with  
25 catchment geodiversity, resulting in strong positive correlations (see Appendix S4). Yet, in the  
26 future, it is important to explore in more detail at which scale geodiversity matters and compare  
27 various approaches of measuring geodiversity (see e.g. Graham *et al.* 2019) to gain better  
28 understanding of the relationship and mechanisms between freshwater biodiversity (measured at  
29 local-scale) and geodiversity (measured across scales from within-waterbody to catchment scales).

30  
31 It is possible that the local physical and chemical variables indicate the conditions of a sampling  
32 time, whereas catchment-scale geodiversity variables are robust to time. Therefore, geodiversity  
33 should represent more exhaustively the variety of factors affecting water quality and physical  
34 environmental conditions within the catchment area (see also Soininen & Luoto, 2012) or reflect the  
35 effects of some latent (e.g., chemical) variables not typically measured in freshwater ecosystems  
36 (Soininen *et al.*, 2015). At catchment scale, habitat and soil heterogeneity caused by  
37 geomorphological and soil features impacts on vegetation cover and surface runoff. This further  
38 creates microhabitats through erosion and accumulation, and affects resources and environmental  
39 conditions resulting, for example, in eutrophication (Carpenter *et al.*, 1998) or brownification  
40 (Kritzberg *et al.*, 2014). The positive effect of geomorphological heterogeneity on aquatic plant  
41 species richness (Fig. 3) suggests that diverse catchment geomorphology creates various abiotic and  
42 biotic conditions and increases the number of habitats (see also Ward *et al.*, 2002; Soininen *et al.*,  
43 2015), but also supports higher resilience towards environmental changes (Piha *et al.*, 2007).  
44 Geomorphological richness measure contains features of various sizes, from small-sized fluvial  
45 features to extensive ridges, which affect catchment hydrology and water-level fluctuation  
46 (Soininen, 2015) as well as seasonal variation and floodplain dynamics (Richards *et al.*, 2002). A  
47 physically more diverse catchment is more likely to support better ecosystem functioning and  
48 higher biodiversity by increased resilience to both external and internal catchment processes, as  
49 well as human activities (see also Ibisate *et al.*, 2011).

1 Interestingly, bedrock variation was often selected in GLMs explaining lake aquatic species  
2 richness, whereas its independent relevance was low (Fig. 4 & 6). It is possible that bedrock acts  
3 behind-the-scenes, by affecting the whole nature of catchments and lakes through mediating water  
4 quality (e.g., carbonate rocks vs. sulphide ore). Yet, confirming the linkage requires closer look on  
5 specific rock types.

## 6 7 **4.2 Comparisons between lakes and rivers**

8 Our second hypothesis (H<sub>2</sub>), where we expected catchment geodiversity to have similar influences  
9 on aquatic plant richness in both lakes and rivers, was partially supported. The most obvious  
10 differences between the habitat types were the weaker overall explanatory power (Table 1) and  
11 higher amount of undetermined variation (Fig. 5) in rivers compared to lakes. This may result from  
12 lower species richness in rivers. For example, susceptibility to disturbances may limit the presence  
13 of some aquatic plants in rivers compared to more stable lakes, resulting in fewer species (Lacoul &  
14 Freedman, 2006).

15  
16 Low explanatory powers of models are common in ecology (Low-Décarie *et al.*, 2014). The  
17 relatively high amount of unexplained variance detected (Fig. 5) is common due to complex nature  
18 of freshwater ecosystems (e.g. Mikulyuk *et al.*, 2011; Alahuhta 2015; Heino *et al.*, 2015). One  
19 possible explanation for this is that it is difficult to include all relevant explanatory variables  
20 affecting different freshwater organism groups. We used the same environmental variables between  
21 lakes and rivers to enable comparison of results between these habitats. However, the low  
22 independent contribution of local variable group and higher unexplained variation in rivers  
23 encourages to consider more habitat-specific approaches. Also, we expect that by capturing some of  
24 the underlying mechanisms behind the detected biodiversity-geodiversity relationships, we could be  
25 able to better consider the causes for the unexplained variance.

26  
27 Of local variables, habitat size had strong independent influences on both lake and river plant  
28 richness (Fig. 6) and it was present in most of the GLMs (Fig. 4). An average trend in habitat size in  
29 our study indicated that both lake surface area and river channel width had a positive association  
30 with species richness. This probably is because there are more habitats existing in larger lakes and  
31 rivers (Heino & Tolonen, 2017). However, the nature of the species-area relationship is known to  
32 vary in different sized and types of lakes (Vestergaard & Sand-Jensen, 2000). Water quality  
33 variables were important for lake all taxa species richness (e.g., alkalinity in BRT and GLM, and  
34 local variable group contribution in VP), whereas contribution of water quality variables to river all  
35 taxa species richness was lower, supporting earlier discussion on more habitat-specific approaches.

## 36 37 **4.3 Observed patterns and differences between the major functional groups**

38 We discovered differences between the two functional groups, as expected (H<sub>3</sub>). In general,  
39 helophyte species richness was better explained than hydrophyte species richness based on higher  
40 explained deviance in GLMs and VP (Table 1, Fig. 5). Geodiversity brought added value to  
41 biodiversity modeling, yet the shared contribution between local and climate variable groups varied  
42 among functional groups and habitats. Observed differences suggest that considering biodiversity  
43 measures, such as functional traits, could guide towards better understanding of ecosystem  
44 processes (incl. aspects of catchment geodiversity) and biodiversity patterns in the changing  
45 environment (see also Alahuhta *et al.*, 2019).

46  
47 Single important explanatory variables varied between the two functional groups. Of local  
48 variables, water colour was highlighted for hydrophytes (negative correlation), whereas climate  
49 variable GDD was pronounced for helophytes (positive correlation) (Fig. 4 & 6, Tables S2.5–S2.6  
50 in Appendix S2). The negative relationship between hydrophyte species richness and colour

1 highlights the fact that there is less light available for submerged taxa in brown-colored waters  
2 (Toivonen & Huttunen, 1995) which seemingly decreases taxon richness. GDD, on the other hand,  
3 represents the strong latitudinal climatic gradient (Pirinen *et al.*, 2012, Tables S2.5–6 in Appendix  
4 S2), indicating that helophyte species richness clearly decreased towards the north. However,  
5 hydrophyte species richness did not follow the same distinct pattern. Yet, it is reasonable to assume  
6 that GDD has the strongest relationship with helophytes that are more directly influenced by  
7 changing air temperatures. In contrast, hydrophytes represent a submerged form of living in less  
8 fluctuating (water) temperatures. Of geodiversity variables, we observed a clear positive  
9 relationship between helophyte species richness and soil variation that potentially links to land use  
10 effects. Helophytes have been found to be favored by eutrophication derived from increased  
11 nutrient concentrations in water (Kolada, 2016), which is a phenomenon connected to land use  
12 (Alahuhta *et al.*, 2016). Further studies on the biodiversity-geodiversity relationships along  
13 changing land-use gradients and different scales (i.e., buffer zone or catchment effect) are thus  
14 needed.

15

#### 16 **4.5 Conclusions**

17 We found a significant positive effect of geodiversity variation (within 1-km<sup>2</sup> grid cells) on aquatic  
18 plant richness. This is the first study that reveals the potential of geodiversity as a surrogate for  
19 aquatic plant species richness analysis at catchment-scale. This finding highlights the fundamental  
20 role of geodiversity in biodiversity conservation and, furthermore, the essence of the CNS approach.  
21 When conserving a lake or a river, we should emphasize freshwater ecosystems whose catchment  
22 areas show high levels of geodiversity, which seem to correlate positively with biodiversity  
23 indicators such as species richness. Then, even if biodiversity was negatively affected by climate  
24 change, greater geodiversity (and more heterogeneous landscape) could potentially lower the risk of  
25 regional population declines under extreme conditions and offer better preconditions for recovery in  
26 the changed environment. This is highly important especially for freshwater ecosystems that are  
27 severely jeopardized by ongoing environmental changes.

28

29 As a next step, we suggest to further test the patterns found in this study in other geographical  
30 locations and at different scales. Despite the importance of catchment area for aquatic ecosystems,  
31 there is a further need to develop local-scale geodiversity indicators measured within and near  
32 aquatic ecosystems. From a conservation perspective, it is relevant to test what type of geodiversity  
33 measures are practical and ecologically suitable (or habitat appropriate) to be applied in  
34 conservation planning, as well as consider additional measures of biodiversity other than species  
35 richness (such as functional diversity).

36

37 Even though methods in science have changed through the ages, many similarities with historical  
38 ideas can still be seen. With his research in *Essay on the Geography of Plants*, von Humboldt's  
39 (1807) intention went beyond the title: his purpose was to show how diverse phenomena of the  
40 world can be unified and reduced to a small set of interconnected patterns. Our study follows  
41 Humboldt's footsteps in that regard. The connection between biodiversity and geodiversity, further  
42 combined to cultural aspects, is indeed a diverse phenomenon. Disentangling this relationship into  
43 finer pieces helps us to understand diversity of life and to protect it for the future.

44

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## Author contributions

Toivanen, Alahuhta, Heino and Hjort designed the research. Toivanen performed the research and the analysis. Tukiainen provided the geodiversity data, and Aroviita provided the river plant data. Toivanen led the writing of the manuscript, with input from Alahuhta, Heino, Hjort, Tukiainen and Aroviita. All authors approved the final manuscript.

## Data availability statement

The lake and river datasets used in this study, including species richness and environmental variables, are provided in Appendix S5 in Supporting Information.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1** Species list and functional groups, descriptive statistics of all variables, and soil-type and rock-type classifications

**Appendix S2** Bivariate correlations of all variables

**Appendix S3** Statistics of GLMs and selected scatterplots

**Appendix S4** Local geodiversity

**Appendix S5** Lake and river datasets

## BIOSKETCH

Maija Toivanen is a geographer interested in geodiversity and its relationship to biodiversity, with special interest in freshwater ecosystems. She is pursuing doctoral degree in physical geography research group in the University of Oulu.

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