RESEARCH PAPER

Journal of Biogeography WILEY

Is catchment geodiversity a useful surrogate of aquatic plant species richness?

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Abstract

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

Location: Finland.

Taxon: Aquatic plants.

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

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

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

1 | INTRODUCTION

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

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

To utilize geodiversity sufficiently as a tool for decision-making and conservation planning, more focused assessments of geodiversity and its relationship with biodiversity are needed (Parks & Mulligan, 2010). In practice, geodiversity data are in many cases easier and less expensive to obtain than biodiversity data (Hjort, Heikkinen, & Luoto, 2012), and the increasing availability of global data sets (e.g. Hengl & Mendes de Jesus, 2017) and various statistical methods (e.g. Bailey, Boyd, & Field, 2018) is making geodiversity mapping possible at different spatial scales. Many studies have recently found that explicit measures of geodiversity can add explanatory power to statistical models accounting for variation in biodiversity (Bailey et al., 2018; Hjort et al., 2012; Tukiainen, Bailey,

et al., 2017a) highlighting the importance of understanding the interactions between biodiversity and Earth surface processes (Antonelli et al., 2018). However, the existing body of research does not yet cover freshwater environments.
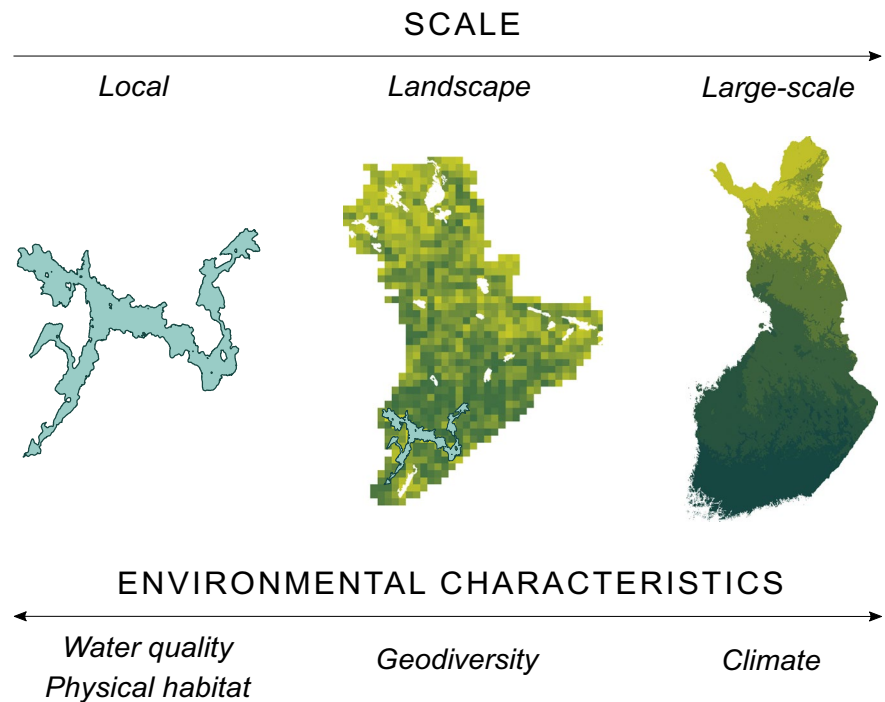
Studies directly linking biodiversity and geodiversity are virtually lacking from freshwaters (but see Kärnä, Heino, Grönroos, & Hjort, 2018 where local-scale in-stream geodiversity measures were applied to explain variation in macroinvertebrate diversity), hindering our possibilities to understand whether geodiversity can be used as a surrogate for biodiversity in the freshwater realm. This deficiency is further emphasized by the fact that, in areas with numerous water bodies, it is challenging to measure direct abiotic characteristics (e.g. water chemistry and local physical habitat) for all water bodies. These characteristics can further vary strongly even between geographically close freshwater systems (Heino et al., 2013; Heino & Tolonen, 2017).

Freshwater ecosystems are shaped by multiple environmental factors operating at various spatial scales, such as water quality at local scale and climate at large scale (Figure 1; Alahuhta et al., 2019; Lacoul & Freedman, 2006). This highlights the importance to consider multi-scale variables affecting these ecosystems (Soininen, Bartels, Heino, Luoto, & Hillebrand, 2015). Catchment (i.e. landscape scale) approach acknowledges the link between aquatic and terrestrial ecosystems, enabling a more comprehensive view on biological communities and ecosystem functions than using local-scale (within-lake or within-river) factors alone (Soininen et al., 2015). It takes a step towards a more process-based approach, recognizing the importance of conserving ecosystem processes instead of individual species or habitats. Catchment properties, such as land cover, topography and geological qualities, have been extensively used to explain water quality and biodiversity in freshwaters (Dodson, Lillie, & Will-Wolf, 2005; Domisch, Amatulli, & Jetz, 2015; Soininen & Luoto, 2012). In contrast, geodiversity represents a more complete characterization of Earth surface heterogeneity compared with coarse topographic variables. As topographic variables may oversimplify the physical environment, geodiversity, in its broadest sense, includes aspects of geology, geomorphology, topography, hydrology and climate (Parks & Mulligan, 2010). Such abiotic heterogeneity relates to extended local-resource gradients, niche space and habitat variety (Matthews, 2014; Stein, Gerstner, & Kreft, 2014). It offers an insight into catchment area heterogeneity which can help reveal factors controlling biodiversity patterns beyond climate and topographic variables.

In this study, we used three explicit geodiversity variables (soil-type richness, rock-type richness and geomorphological richness) that have been developed and studied rather extensively in terrestrial landscapes (Hjort et al., 2012; Hjort & Luoto, 2010; Tukiainen,

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. Alahuhta et al., 2019; Lacoul & Freedman, 2006). The visualized geodiversity variable is geomorphological richness and the climate variable is growing degree-days across Finland. [Colour figure can be viewed at wileyonlinelibrary.com]

SCALE

Local   Landscape   Large-scale

ENVIRONMENTAL CHARACTERISTICS

Water quality   Geodiversity   Climate
Physical habitat

Bailey, et al., 2017a) in relation to human impact (Räsänen et al., 2016; Tukiainen, Alahuhta, et al., 2017b) and scale-related influences (Bailey, Boyd, Hjort, Lavers, & Field, 2017). Our overall aim was to investigate whether geodiversity could act as a surrogate for aquatic plant species richness in two different freshwater habitats (i.e. lakes and rivers). More precisely, we studied: (a) how does a set of three environmental variables (local, geodiversity, climate) explain patterns in species richness of aquatic plants, (b) do the detected patterns in aquatic plant species richness vary between the lakes and rivers and (c) do different functional plant groups (i.e. helophytes vs. hydrophytes) respond differently to local, geodiversity and climate variables?

To disentangle the first study question, we focused on a variety of local and climate variables that are known to affect aquatic plant species richness (Akasaka & Takamura, 2011; Alahuhta, 2015; Toivonen & Huttunen, 1995; Vestergaard & Sand-Jensen, 2000), in addition to geodiversity variables that represent a novel aspect in modelling freshwater biodiversity. First (H_1), we hypothesized that catchment geodiversity brings added value to modelling aquatic plant richness based on outcomes derived from terrestrial plants (Bailey et al., 2018; Tukiainen, Alahuhta, et al., 2017b; Tukiainen, Bailey, et al., 2017a). However, we expected local variables to contribute most strongly to aquatic plant species richness, because water quality and physical habitat conditions are often key environmental factors structuring aquatic plant communities (Alahuhta, 2015; Vestergaard & Sand-Jensen, 2000; Viana et al., 2014). Second (H_2), we expected catchment geodiversity to have a similar influence on aquatic plant species richness in lakes and rivers, because catchment geological and geomorphological qualities similarly provide a base for the key habitat factors influencing aquatic plants (e.g. water chemistry and land cover; Lacoul & Freedman, 2006). Third (H_3), we

assumed to find differences between functional groups in their response to environmental variables, because helophytes and hydrophytes differ in their accessibility to carbon and nutrient storages, and may thus show different responses to water quality and hydromorphological variables (Akasaka, Takamura, Mitsuhashi, & Kadono, 2010; Alahuhta et al., 2014; Kolada, 2016; Toivonen & Huttunen, 1995).

2 | MATERIALS AND METHODS

2.1 | Aquatic plant data

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

Lake plants were surveyed using a main belt transect method (Leka et al., 2003). Transects are 5-m-wide sections positioned perpendicularly to the shoreline. Each transect extends from the upper eulittoral to the outer depth limit of vegetation, or to the deepest point of the basin if vegetation covers the entire lake. Transects were divided into zones according to the dominant life-form or dominant species, and frequency and cover of each species were recorded. Plants were observed by wading or by boat, with the aid of rake and hydroscope. River plants were sampled using
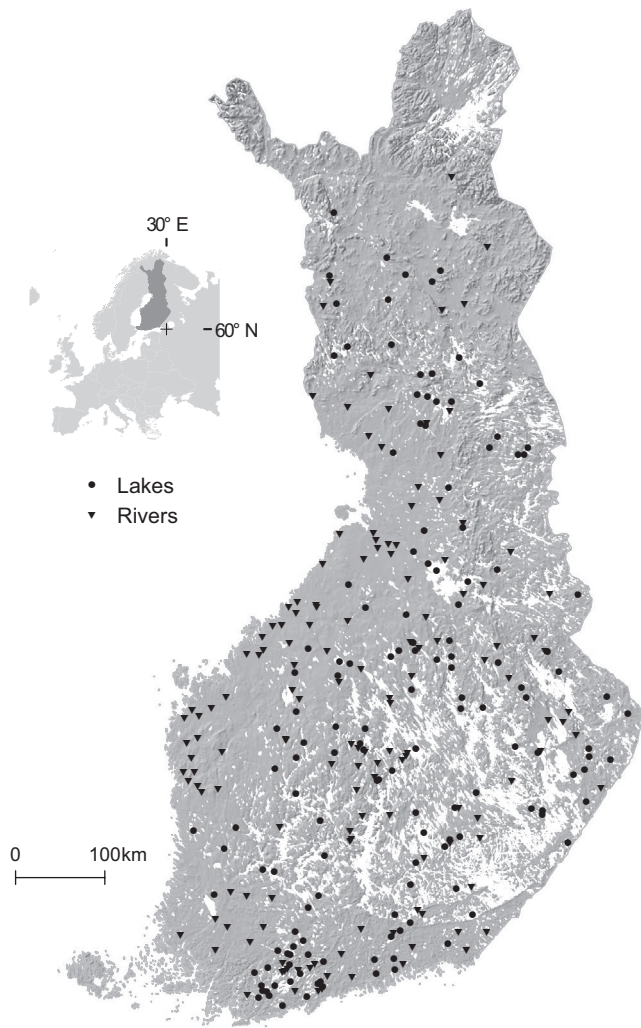
FIGURE 2 Sampled lakes (*n* = 145) and river reaches (*n* = 146). The grey background is a hillshade image visualizing topography of Finland (National Land Survey of Finland). Lakes on the map are shown in white.

national version of the methodology based on international standard SFS-EN 14184 (Rääpysjärvi, Hämäläinen, & Aroviita, 2016). At each study reach, two 100-m sections, a riffle section and a pool section, were surveyed. Each 100-m section was divided into five 20-m-long subsections, where abundance and frequency of each vascular plant species were estimated. River plants were observed by wading with the aid of rake. Due to the different plant survey methods, lake and river data sets could not be pooled together, and we, therefore, studied lake and river plants separately. We used presence–absence data of lake and river plant species in the statistical analysis

2.2 | Environmental data

We used three sets of environmental variables as predictors of aquatic plant species richness: (a) local, (b) catchment geodiversity and (c) climate variables. Descriptive statistics are presented in Appendix S1 (Table S1.3).

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

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

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

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

Prior to further data analysis, we explored Spearman correlations (*R*$_S$) between pairs of predictor variables to avoid multicollinearity at the level of *R*$_S$ |>0.7|, following Dormann et al. (2013). Final variables were selected based on bivariate correlations and conceptual relevance (correlations presented in Tables S2.5–S2.6 in Appendix S2). For geodiversity variables, we considered both mean and standard deviation values, because catchment areas vary in size among lakes and rivers. Altogether, final data analysis included alkalinity, lake area (lakes), channel width (rivers), colour, total phosphorous (TP),

standard deviation of soil richness (SoilStd), standard deviation of rock richness (RockStd) and standard deviation of geomorphological richness (GMStd).

2.3 | Statistical methods

We generated generalized linear models (GLMs) for the richness of all taxa, helophytes and hydrophytes to identify important predictor variables separately for lakes and rivers using the 'dredge' function in the R (R Development Core Team, 2008) package 'MuMIn' (Barton, 2017). We used Gaussian or Poisson error distribution (with log link function) in the model fitting, and calculated adjusted explained deviance (adj. D^2) values for each model with R package 'modEvA' (Barbosa, Brown, Jimenez-Valverde, & Real, 2016). Poisson error distribution was used with river hydrophyte richness and Gaussian error distribution with all other response variables. Models were ranked by corrected Akaike information criterion (AICc) values with a cut-off level of $\Delta < 2$. AICc is corrected for small sample size and considers sample size by increasing the relative penalty for model complexity with small data sets. Models with AICc differing by <2 are typically considered to have similar statistical support. This analysis also produces Akaike weights, which reflect the relative support for each model within AICc ranked models scaled to 0–1 (least to highest) (Burnham & Anderson, 2004). Sum of weights of ranked models ($\Delta < 2$) is 1. From here, we refer to best models as the ones with the lowest delta value and largest weight value among the ranked models.

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

We used variation partitioning (VP, Legendre & Legendre, 2012) following the approach of Hawkins, Porter, and Diniz-Filho (2003) to measure the independent and shared contributions of the local, geodiversity and climate environmental variable groups in explaining variation in aquatic plant richness in lakes and rivers. Consequently, we formed seven GLMs using (a) local, (b) geodiversity, (c) climate, (d) local and geodiversity, (e) local and climate, (f) geodiversity and climate variables and (g) all variables from all three groups. Based on adjusted D^2 values extracted from these seven separate GLMs, we calculated the independent and shared fractions for the three explanatory variable groups. Adjusted D^2 values account for different number or environmental variables in different variable groups (Guisan & Zimmermann, 2000). We used both linear and quadratic terms of the explanatory variables to capture the potential nonlinear responses.

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

3 | RESULTS

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

3.1 | Generalized linear models

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

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

We checked the residuals of the best models for spatial autocorrelation (Figure S3.1 in Appendix S3). In four models (lake hydrophyte, river all taxa, river helophyte and river hydrophyte species richness), there were statistically significant ($p < 0.05$) spatial autocorrelations detected with low p-values and within various distances, suggesting no serious bias by spatial autocorrelation (see Hawkins, Diniz-filho, Bini, Marco, & Blackburn, 2007). Spatial patterns in our data set closely reflected the inherent latitudinal climate gradient extending across the study area.

3.2 | Variation partitioning

In the GLM-based VP (Figure 5), either local or geodiversity variable group had the highest explanatory power in each data set when looking solely at their independent contributions. Relatively, climate variable group contributed mostly to helophyte species richness both in lake and river data sets. Highest shared contribution was between local and geodiversity variable groups, except for river
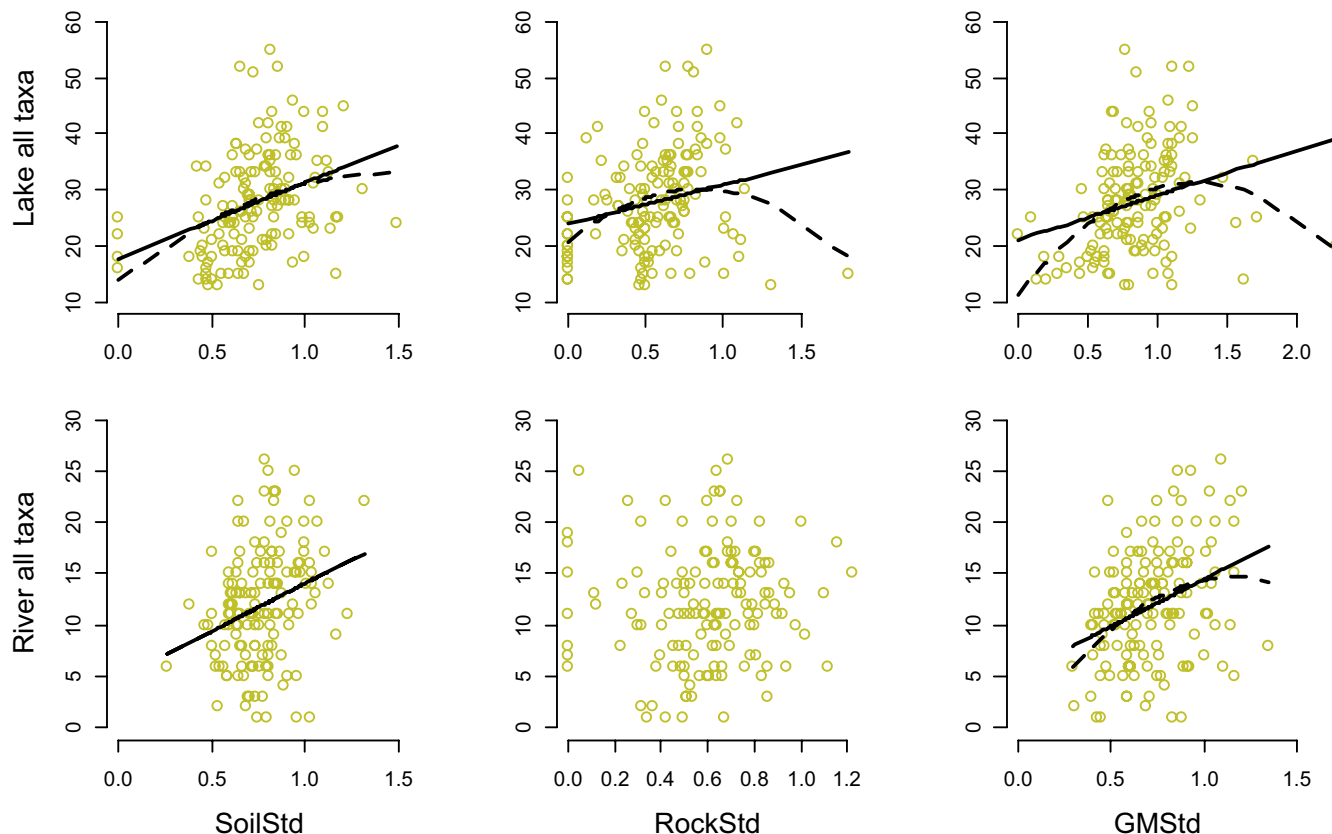
FIGURE 3 Scatterplots of species richness of aquatic plants in Finland and geodiversity (standard deviation values) variables. Regression lines are (solid for linear, dashed for quadratic terms) fitted if statistically significant ($p < 0.001$). Scatterplots of local and climate variables are presented in Appendix S3 (Figure S3.2). See Section 2.2 for abbreviations. [Colour figure can be viewed at wileyonlinelibrary.com]

helophyte species richness, where the highest shared contribution was the one between geodiversity and climate variable groups. Undetermined variation varied between 40.3%–56.8% in lakes and 76.5%–83.5% in rivers.

3.3 | Boosted regression trees

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

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

4 | DISCUSSION

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

4.1 | Linking geodiversity to aquatic plant species richness

First, we wanted to find out how well local, climate and geodiversity variables explain variation in species richness of aquatic plants. We found support for our first hypothesis (H_1) as geodiversity variables brought added value to the modelling of aquatic plant richness. For instance, geodiversity variable group had the largest independent
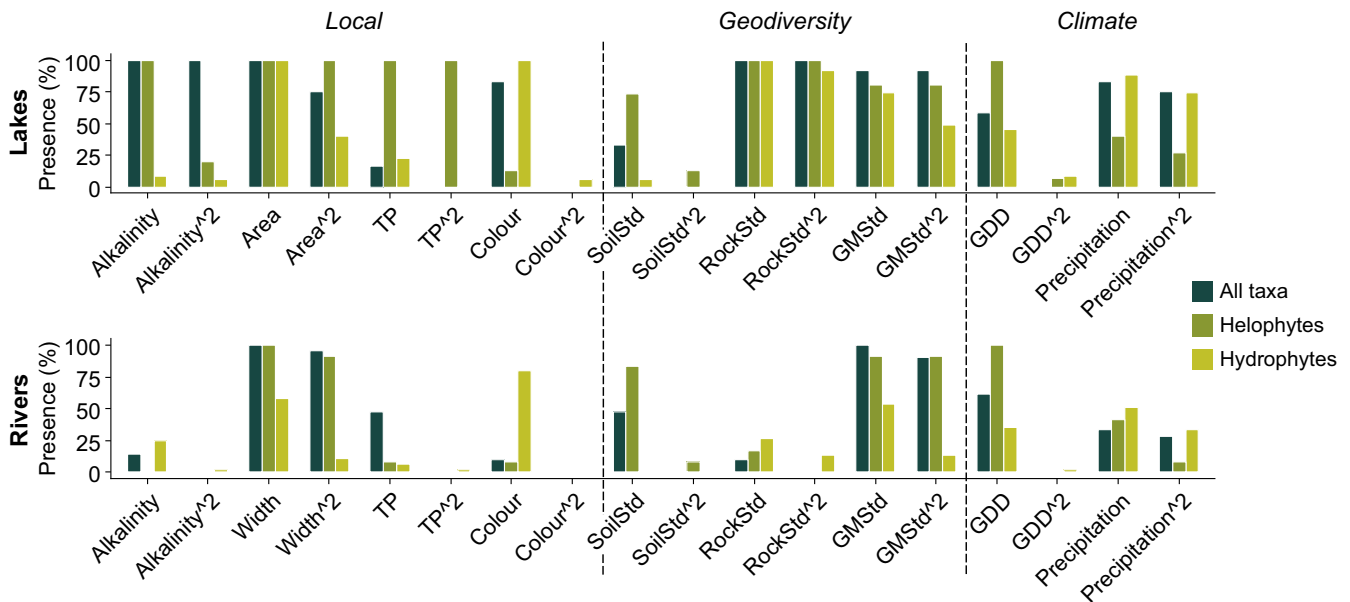
FIGURE 4 Variables (linear and quadratic (^2) terms) present in generalized linear models explaining lake species richness (out of 12, 15, 35 models for all taxa, helophyte and hydrophyte species richness, respectively) and river species richness (out of 21, 12, 45 models for all taxa, helophyte and 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. [Colour figure can be viewed at wileyonlinelibrary.com]

contribution to species richness of all taxa in both lakes and rivers (Figure 5). Also, local variables contributed rather strongly to aquatic plant richness, as expected. Both habitat size (lake surface area and river channel width) and water quality (alkalinity, colour and TP) variables explained species richness relatively well, but the best models were achieved when geodiversity variables were present together with local and/or climate variables.

Our results are generally in line with previous studies with similar geodiversity variables from the terrestrial realm (Bailey et al., 2018; Hjort et al., 2012; Räsänen et al., 2016; Tukiainen, Bailey, et al., 2017a). In the recent study by Kärnä et al. (2018), local-scale in-stream geodiversity variables were found to complement traditional physical habitat and water quality variables in accounting for macroinvertebrate diversity. The methods and taxonomic group in the study by Kärnä et al. (2018) were vastly different from ours in quantifying in-stream geodiversity. However, the results align with our catchment-scale approach, suggesting that both landscape and local-scale geodiversity are important for freshwater biodiversity. Furthermore, similar results have now been presented for aquatic plants (our study), terrestrial vascular plants (e.g. Bailey et al., 2017; Tukiainen, Bailey, et al., 2017a) and stream macroinvertebrates (Kärnä et al., 2018). Correspondingly, Antonelli et al. (2018) found soil heterogeneity and topographic relief to be strong predictors of various taxa in mountains both at global and regional scales.

Throughout the study, aquatic plant richness and geodiversity mostly showed a positive relationship, with some indications of negative hump-shaped responses (Figure 3). In particular, we applied standard deviation values of geodiversity that represent the variation in geodiversity across catchment areas. This, in turn, is related to abiotic environmental heterogeneity. Both positive and

unimodal responses have been observed in earlier research on the relationship between species richness and environmental heterogeneity (Stein et al., 2014). However, environmental heterogeneity often scales positively with area, thus making it difficult to detect the individual effects of environmental heterogeneity and area (see Stein et al., 2014). We studied catchment areas with varying size (Table S1.3 in Appendix S1), but calculated mean and standard deviation values from gridded geodiversity data to account for the well-known area effect. In our data, geodiversity (std values) was positively correlated with catchment area size, yet correlation was rather weak ($r = 0.115$–0.384, Tables S2.5–2.6 in Appendix S2), suggesting that different size catchments should be studied separately. Naturally, larger catchments potentially hold higher geodiversity. However, catchment processes are an integral part of freshwater biodiversity and water quality (Dodson et al., 2005; Soininen et al., 2015; Soininen & Luoto, 2012) through interaction with local-scale processes. Complementarily, we explored the relationship between local (within shoreline) geodiversity with catchment geodiversity, resulting in strong positive correlations (see Appendix S4). Yet, in the future, it is important to explore in more detail at which scale geodiversity matters and compare various approaches of measuring geodiversity (see e.g. Graham, Spake, Gillings, Watts, & Eigenbrod, 2019) to gain better understanding of the relationship and mechanisms between freshwater biodiversity (measured at local scale) and geodiversity (measured across scales from within-water body to catchment scales).

It is possible that the local physical and chemical variables indicate the conditions of a sampling time, whereas catchment-scale geodiversity variables are robust to time. Therefore, geodiversity should represent more exhaustively the variety of factors affecting
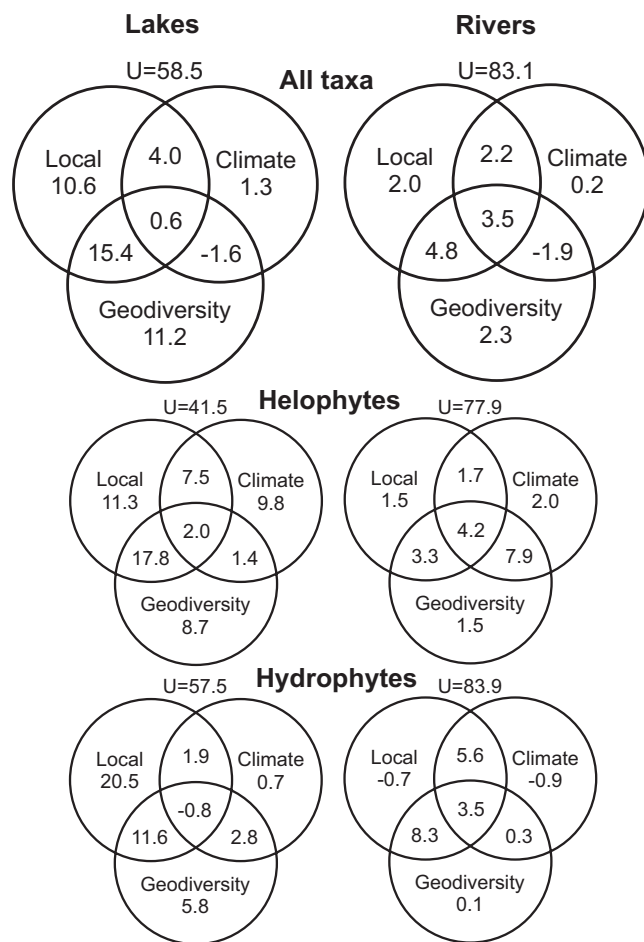
FIGURE 5 Results of the variation partitioning, in terms of proportions of deviance accounted for (%) in aquatic plant richness in Finland, separated into the independent contributions (geodiversity, local and climate), the shared contributions and the undetermined variation (U). The negative shared 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, colour, TP, area (for lakes) and width (for rivers). Climate variables were GDD and precipitation. See Section 2.2 for abbreviations.

water quality and physical environmental conditions within the catchment area (see also Soininen & Luoto, 2012) or reflect the effects of some latent (e.g. chemical) variables not typically measured in freshwater ecosystems (Soininen et al., 2015). At catchment scale, habitat and soil heterogeneity caused by geomorphological and soil features impacts on vegetation cover and surface runoff. This further creates microhabitats through erosion and accumulation, and affects resources and environmental conditions resulting, for example, in eutrophication (Carpenter et al., 1998) or brownification (Kritzberg et al., 2014). The positive effect of geomorphological heterogeneity on aquatic plant species richness (Figure 3) suggests that diverse catchment geomorphology creates various abiotic and biotic conditions and increases the number of habitats (see also Soininen et al., 2015; Ward, Tockner, Arscott, & Claret, 2002), but also

supports higher resilience towards environmental changes (Piha, Luoto, Piha, & Merilä, 2007). Geomorphological richness measure contains features of various sizes, from small-sized fluvial features to extensive ridges, which affect catchment hydrology and water-level fluctuation (Soininen, 2015) as well as seasonal variation and flood-plain dynamics (Richards, Brasington, & Hughes, 2002). A physically more diverse catchment is more likely to support better ecosystem functioning and higher biodiversity by increased resilience to both external and internal catchment processes, as well as human activities (see also Ibisate, Ollero, & Díaz, 2011).

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

4.2 | Comparisons between lakes and rivers

Our second hypothesis (H$_2$), where we expected catchment geodiversity to have similar influences on aquatic plant richness in both lakes and rivers, was partially supported. The most obvious differences between the habitat types were the weaker overall explanatory power (Table 1) and higher amount of undetermined variation (Figure 5) in rivers compared to lakes. This may result from lower species richness in rivers. For example, susceptibility to disturbances may limit the presence of some aquatic plants in rivers compared to more stable lakes, resulting in fewer species (Lacoul & Freedman, 2006).

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

Of local variables, habitat size had strong independent influences on both lake and river plant richness (Figure 6) and it was present in most of the GLMs (Figure 4). An average trend in habitat size in our study indicated that both lake surface area and river channel width had a positive association with species richness. This probably is because there are more habitats existing in larger lakes and rivers (Heino & Tolonen, 2017). However, the nature of the species–area relationship is known to vary in different sized and types of lakes
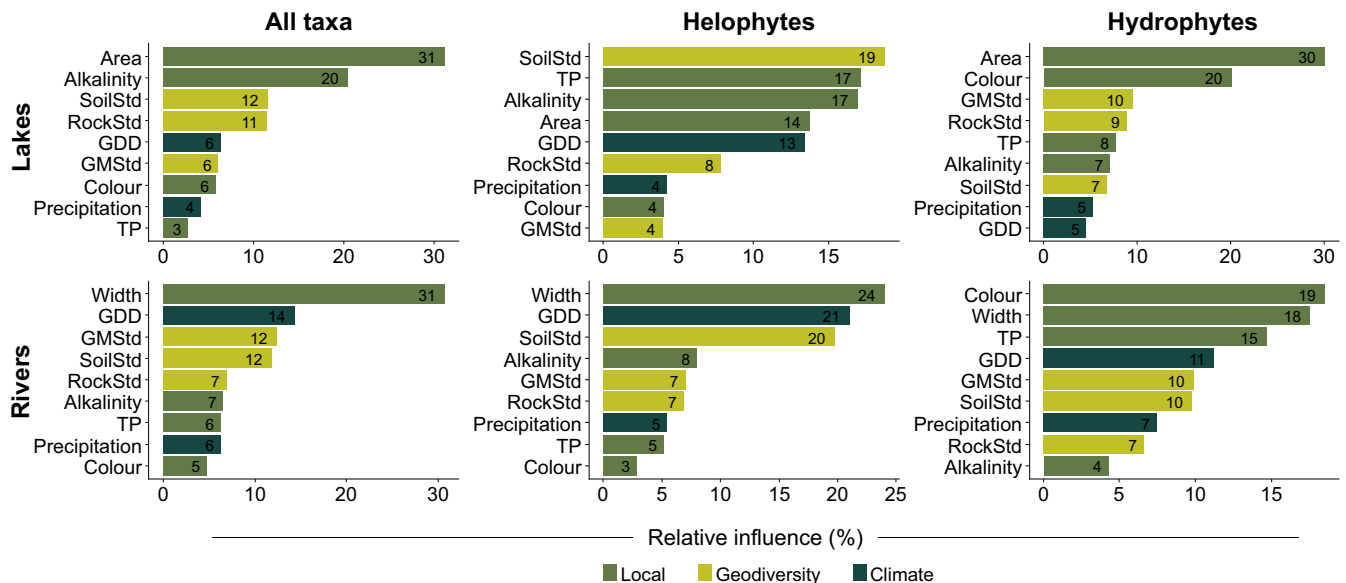
FIGURE 6 The relative influence (%) of individual variables from the boosted regression tree analysis. Exact values for each variable are given inside the bars. All taxa, helophytes and hydrophytes refer to aquatic plant species richness in Finland. See Section 2.2 for abbreviations. [Colour figure can be viewed at wileyonlinelibrary.com]

(Vestergaard & Sand-Jensen, 2000). Water quality variables were important for lake all taxa species richness (e.g. alkalinity in BRT and GLM, and local variable group contribution in VP), whereas contribution of water quality variables to river all taxa species richness was lower, supporting earlier discussion on more habitat-specific approaches.

4.3 | Observed patterns and differences between the major functional groups

We discovered differences between the two functional groups, as expected (H₃). In general, helophyte species richness was better explained than hydrophyte species richness based on higher explained deviance in GLMs and VP (Table 1, Figure 5). Geodiversity brought added value to biodiversity modelling, yet the shared contribution between local and climate variable groups varied among functional groups and habitats. Observed differences suggest that considering biodiversity measures, such as functional traits, could guide towards better understanding of ecosystem processes (including aspects of catchment geodiversity) and biodiversity patterns in the changing environment (see also Alahuhta et al., 2019).

Single important explanatory variables varied between the two functional groups. Of local variables, water colour was highlighted for hydrophytes (negative correlation), whereas climate variable GDD was pronounced for helophytes (positive correlation) (Figure 4 and 6, Tables S2.5–S2.6 in Appendix S2). The negative relationship between hydrophyte species richness and colour highlights the fact that there is less light available for submerged taxa in brown-coloured waters (Toivonen & Huttunen, 1995) which seemingly decreases taxon richness. GDD, on the other hand, represents the strong latitudinal climatic gradient (Pirinen et al., 2012, Tables

S2.5–6 in Appendix S2), indicating that helophyte species richness clearly decreased towards the north. However, hydrophyte species richness did not follow the same distinct pattern. Yet, it is reasonable to assume that GDD has the strongest relationship with helophytes that are more directly influenced by changing air temperatures. In contrast, hydrophytes represent a submerged form of living in less fluctuating (water) temperatures. Of geodiversity variables, we observed a clear positive relationship between helophyte species richness and soil variation that potentially links to land-use effects. Helophytes have been found to be favoured by eutrophication derived from increased nutrient concentrations in water (Kolada, 2016), which is a phenomenon connected to land use (Alahuhta, Luukinoja, Tukiainen, & Hjort, 2016). Further studies on the biodiversity–geodiversity relationships along changing land use gradients and different scales (i.e. buffer zone or catchment effect) are thus needed.

4.4 | Conclusions

We found a significant positive effect of geodiversity variation (within 1-km² grid cells) on aquatic plant richness. This is the first study that reveals the potential of geodiversity as a surrogate for aquatic plant species richness analysis at catchment scale. This finding highlights the fundamental role of geodiversity in biodiversity conservation and, furthermore, the essence of the CNS approach. When conserving a lake or a river, we should emphasize freshwater ecosystems whose catchment areas show high levels of geodiversity, which seem to correlate positively with biodiversity indicators such as species richness. Then, even if biodiversity was negatively affected by climate change, greater geodiversity (and more heterogeneous landscape) could potentially lower the risk of regional population declines under extreme conditions and offer better preconditions for recovery in the changed

environment. This is highly important especially for freshwater ecosystems that are severely jeopardized by ongoing environmental changes.

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

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

ACKNOWLEDGEMENTS

DATA AVAILABILITY STATEMENT

The lake and river data sets used in this study, including species richness and environmental variables, are provided in Appendix S5.

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SUPPORTING INFORMATION

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