

**Spatial relationship between biodiversity and geodiversity across a gradient of land-use  
intensity in high-latitude landscapes**

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## Abstract

*Context.* ‘Conserving Nature’s stage’ has been advanced as an important conservation principle because of known links between biodiversity and abiotic environmental diversity, especially in sensitive high-latitude environments and at the landscape scale. However these links have not been examined across gradients of human impact on the landscape.

*Objectives.* To (1) analyze the relationships between land-use intensity and both landscape-scale biodiversity and geodiversity, and (2) assess the contributions of geodiversity, climate and spatial variables to explaining vascular plant species richness in landscapes of low, moderate and high human impact.

*Methods.* We used generalized additive models (GAMs) to analyze relationships between land-use intensity and both geodiversity (geological, geomorphological and hydrological richness) and plant species richness in 6191 1-km<sup>2</sup> grid squares across Finland. We used linear regression-based variation partitioning (VP) to assess contributions of climate, geodiversity and spatial variable groups to accounting for spatial variation in species richness.

*Results.* In GAMs, geodiversity correlated negatively, and plant species richness positively, with land-use intensity. Both relationships were non-linear. In VP, geodiversity best accounted for species richness in areas of moderate to high human impact. These overall contributions were mainly due to variation explained jointly with climate, which dominated the models. Independent geodiversity contributions were highest in pristine environments, but low throughout.

*Conclusions.* Human action increases biodiversity but may reduce geodiversity, at landscape scale in high-latitude environments. Better understanding of the connections between biodiversity and abiotic environment along changing land-use gradients is essential in developing sustainable measures to conserve biodiversity under global change.

**Keywords:** hemeroby, species richness, human impact, variation partitioning, boreal, sub-Arctic

## Introduction

30 Global change is affecting life on Earth, often negatively. This trend is not slowing down (Butchart et al 2010), so more attention is being paid to conserving landscapes and related processes instead of individual properties therein, such as single species and geological formations (Lindenmayer et al 2008; Anderson and Ferree 2010; Comer et al 2015). This is especially relevant in boreal and Arctic areas, which are increasingly becoming focal points of  
35 environmental, economic and geopolitical interest (Young 2012), leading to intensified land use and increased human pressures in these high-latitude landscapes. Even without human impact, high-latitude ecosystems are sensitive to climate warming because of their marginal locations and the fact that the projected rises in temperature increase poleward (IPCC 2013). Ecological changes driven by environmental change have already occurred in Arctic areas,  
40 and vegetation responses to global warming may be complex (Post et al 2009). In facing future challenges in environmental conservation and land-use planning, profound knowledge of the factors affecting biodiversity across high-latitude landscapes is essential.

One of the biggest threats to landscape-scale conservation is land-use change, modifying natural and semi-natural environments to more anthropogenic landscapes  
45 (Vitousek et al 1997). Natural and semi-natural environments are increasingly concentrated in remote areas, not least in the high latitudes (Matthews 1983; Foley et al 2005). In semi-natural landscapes, land use has not radically changed biological, geological and hydrological conditions, whereas in urban and intensive agricultural environments these biotic and abiotic characteristics have been severely modified, fundamentally shifting the whole ecosystem  
50 (Brown et al 2005; Wu et al 2011; Newbold et al 2015). Results include fewer habitats and the fragmentation of remaining semi-natural habitats in many landscapes (Wilson et al 2016).

Indeed, many now argue that human activities have caused the Earth to enter a new, human-dominated geological epoch, the so-called Anthropocene (Lewis and Maslin 2015).

The influence of land use on biodiversity has been intensively studied (e.g. McKinney 2004; Flynn et al 2009), but much less is known about how land-use changes affect diversity patterns of abiotic features – geodiversity (Gray 2013). Geodiversity is commonly defined as the variety of earth surface materials, forms and processes (geological, geomorphological and hydrological). More simply, it is the abiotic richness of Earth surface (Gray 2013).

Geodiversity forms a basis for biological diversity because organisms depend on abiotic components. For example, different habitats result from different geological attributes, landforms and processes; and abiotic components of ecosystems influence micro-climates, control hydrology, facilitate nutrient cycling and create niche space (Nichols et al 1998; Matthews 2014; Lawler et al 2015). At the landscape scale, higher geodiversity enables more niches within the same environment, allowing a higher degree of biodiversity to co-exist (Parks and Mulligan 2010; Matthews 2014). However, despite the intimate links between geodiversity and biodiversity, conservation approaches have typically neglected geodiversity (Anderson and Ferree 2010; Gray 2013; Matthews 2014).

Recently, the concept of geodiversity has been put forward as a novel, potentially useful approach to explore and understand biodiversity, complementary to existing approaches (Gray et al 2013; Lawler et al 2015). With respect to conservation, the concept of “conserving Nature’s stage” (CNS) has emerged (Lawler et al 2015), which encapsulates the idea that maintaining a varied physical landscape will enable diverse ecological processes to operate, both protecting and promoting biodiversity. Within this framework, geodiversity can act as a coarse-filter strategy for conserving ecological and evolutionary processes and biodiversity.

Species richness, the number of different species within the study unit (Purvis and Hector 2000), is the most commonly used measure of plant biodiversity and is the focus of

considerable theoretical interest (Field et al 2009). Given the large grain and extent of our study, it was also the only biodiversity measure available to us. Species richness is known to correlate with various environmental gradients (Field et al 2009), but much less is known about its relationship with geodiversity. Globally, regions with highest plant species richness have been found to be parts of the tropics with steep climatic gradients, diverse edaphic structures and high topographic heterogeneity (Mutke and Barthlott 2005; Lawler et al 2015). Geomorphological heterogeneity has been shown to promote higher plant species richness at the landscape scale (Nichols et al 1998). At local scales, landslides (Alexandrowicz and Margielewski 2010), earth surface processes (le Roux and Luoto 2014) and geological substrates (Kougioumoutzis and Tiniakou 2015) can, for example, be important determinants of terrestrial plant distributions. However, plant species richness has rarely been associated with geodiversity measured as multiple geological, geomorphological and hydrological features (for an exception, see Hjort et al 2012). Few studies have mapped correlations between plant species richness and individual geological, geomorphological or hydrological features, at any scale. Importantly, the relationship between plant species richness and geodiversity has never been studied along a land-use intensity gradient, despite the importance of global land-use intensification.

In the face of the global change, it is essential to find appropriate ways of modelling species' diversity and distributions (Guisan and Zimmerman 2000). According to CNS, it is important to establish whether information on geodiversity can be utilized for biodiversity models and conservation. Since global biodiversity conservation depends increasingly on maintaining biodiversity in human-dominated landscapes (Fahrig et al 2011), we must examine this relationship in environments of varying human impact. Thus, in this study, we 1) analyze the landscape-scale relationships between land-use intensity and both geodiversity, biodiversity; and 2) determine the relative contributions of geodiversity, climate and spatial

variables in explaining vascular plant species richness in environments of weak, moderate and high human impact.

More specifically, we seek answers to two main questions. (1) What is the relationship between land-use intensity and each diversity measure? For species richness, the intermediate disturbance hypothesis (Connell 1978) predicts a unimodal (humped) relationship. Further, biodiversity can be high in agricultural and semi-urban environments, where favourable environmental conditions and introduction of alien species increase species richness (Landsberg 1981; McKinney 2002; Kühn and Klotz 2006), while human disturbances are not (yet) extreme. For geodiversity, we have no theoretical prediction, but human actions may tend to concentrate in areas of moderate geodiversity (e.g. agriculture is often in quite abiotically diverse river valleys), while areas with the highest geodiversity (e.g. mountainous environments and high-energy coasts; Gray 2008; Serrano et al 2009; Hjort and Luoto 2010) are often not very suitable for human settlements and actions. Conversely, human actions tend to reduce geodiversity (e.g. smaller landforms and hydrological features are destroyed during ground levelling and excavation; Gordon and Barron 2013). Thus, a humped relationship may be expected. (2) Do measures of geodiversity account for the variation in plant species richness patterns best in areas of lowest human impact? Preliminary results from Hjort et al (2012) and Räsänen et al (2016) suggest this.

## Methods

### *Study area*

The study area consisted of 6191 1-km<sup>2</sup> grid cells dispersed across Finland (approximately 60°–70° N and 20°–31° E; Fig. 1). These grid cells include a wide variety of abiotic earth-surface features. The landscapes of the study area vary from fertile, deciduous forests in the south to more barren, northern boreal coniferous forests and fell areas with Arctic conditions

in the north. Most of the study area is covered with weakly and moderately human-impacted land, with only 7.5% of strongly human-impacted areas, located mainly around cities and municipality centres (Fig. 1).

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#Figure 1 approximately here#

In the study area, the mean annual air temperature varies approximately between  $-2.9^{\circ}\text{C}$  and  $6.4^{\circ}\text{C}$ , from north to south (Table 1). Precipitation is moderate in all seasons, ranging annually between 410 and 750 mm. Geologically, Finland is a part of the Precambrian bedrock block of northern and eastern Europe. The bedrock consists mainly of crystalline rocks like schists, gneisses and granites (Atlas of Finland 1990a). The soil features dominating the landscape are ground moraine, sand, gravel and peat deposits (Atlas of Finland 1990b; Seppälä 2005). Geomorphological features, such as glaciofluvial (e.g. eskers) and glacial (e.g. drumlins) forms, are common across the country (Atlas of Finland 1986).

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#Table 1 approximately here#

### *Species richness data*

The total number of vascular plant species recorded in each 1-km<sup>2</sup> grid cell was used as a measure of biodiversity (Fig. 2). Because of long-term botanical tradition, the distribution patterns of vascular plant species are relatively well known across the study area. The vascular plant data we used are maintained by the Finnish Museum of Natural History (Lampinen et al 2012), and comprise the presence records of all observed vascular plant species in each inventoried grid cell, based on censuses carried out between 1985 and 2011. A total of 2108 vascular plant taxa were recorded and used in this study (including subspecies

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and hybrids, e.g. Thuiller et al 2006). The number of species in a grid cell varied from 30 to 434. All the cells whose area was at least 80% land (i.e. maximum 20% water) were included in our analyses.

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#Figure 2 approximately here#

### *Land-use intensity*

The land-use intensity assessment we used is based on the concept of hemeroby (closeness to nature, degree of naturalness), first introduced by the botanist Jalas (1955). Hemeroby is an integrative measure of the impact of all human intervention on ecosystems, measuring the distance between the current vegetation and the potential natural vegetation of the site with no human intervention (Paracchini and Capitani 2011; Walz and Stein 2014). Hemeroby has been used in several contexts to evaluate and compare landscapes and to measure the degree of artificiality (e.g. Hill et al 2002; Szilárd 2009; Paracchini and Capitani 2011).

We created a landscape-scale hemeroby classification to measure human intervention in land use (Fig. 2). Land use was classified into seven classes: 1. ahemerobic (almost no human impacts), 2. oligohemerobic (weak human impacts), 3. mesohemerobic (moderate human impacts), 4.  $\beta$ -euhemerobic (moderate-strong human impacts), 5.  $\alpha$ -euhemerobic (strong human impacts), 6. polyhemerobic (very strong human impacts) and 7. metahemerobic (extremely strong human impacts). The classification was based on the European land-cover and land-use classification 'CORINE' (Coordination of Information on the Environment – Land Cover 2006) at 25-m resolution, following Walz and Stein (2014). In the cases of the CORINE classes “coniferous forest” and “mixed forest”, the classification was improved using information on tree stand age (Luke 2011) and protected area status (Finnish Environment Institute 2013a). Specifically, if a tree stand was more than 80 years old or if the



forest is inside a protected area, the tree stand pixel was classified as oligohemerobic (class 2, weak human impacts); otherwise it was classified as mesohemerobic (class 3, moderate human impacts). Water areas were excluded (see Appendix 2 for more details of the classification). For local-scale or temporal analysis, the hemeroby index could be further improved by using spatially and thematically more accurate, up-to-date habitat data instead of general land-use classification (e.g. Walz and Stein 2014).

After creating a grid of hemeroby that covered the whole study area, we calculated a simple area-weighted hemeroby index for 1-km<sup>2</sup> grid cells following Walz and Stein (2014):

$$M = \sum_{h=1}^n f_n * h$$

where  $M$  is hemeroby index,  $n$  is the number of classes of hemeroby (here:  $n = 7$ ),  $f_n$  is the proportion of category  $n$  and  $h$  is the class of hemeroby. The maximum value of  $M$  (7) can be obtained when the whole grid cell comprises metahemerobic land use (class 7 – extremely strong human impacts), and the minimum value (1) described cells entirely comprising areas of almost no human impacts (ahemerobic, class 1).

For use in variation partitioning analysis, we divided the grid cells into three categories of land-use intensity, based on  $M$ :  $M < 3$  = category 1 (low human impacts);  $3 \leq M < 5$  = category 2 (moderate human impacts);  $M \geq 5$  = category 3 (high human impacts). From each of these three categories, 467 grid cells were randomly sampled for further analysis (variation partitioning), to maintain comparability among the data; 467 was the minimum number of cells in a category (category 3).

### *Environmental variables*

Three sets of environmental variables were used as predictors for vascular plant species richness: (i) climate, (ii) geodiversity and (iii) spatial variables. Climate variables have been

commonly used to predict and model the diversity of vascular plants at landscape scales (Field et al 2009), whereas geodiversity variables represent a novel, understudied group of abiotic predictors (Hjort et al 2015). We included spatial variables to account for spatially structured variation attributable to unmeasured influences, such as dispersal limitation or unmeasured environmental variables (Dray et al 2012).

Climate variables compiled for this study were mean annual air temperature, annual temperature sum above 5°C (i.e. growing degree days, GDD), mean annual precipitation, potential evapotranspiration, water balance and theoretical solar radiation (Table 1). The data were derived from the Finnish Meteorological Institute (Pirinen et al 2012) and digital elevation models (NLS 2000). Mean annual air temperature, GDD and mean annual precipitation were calculated in ArcMap 10.2 from time period of 1981–2010, from monthly (temperature, precipitation) or daily (GDD) data. Potential evapotranspiration from the same time period was calculated following Skov and Svenning (2004):

$$PET = 58.93 * T_{above0} / 12$$

Water balance was calculated as the monthly difference between precipitation and potential evapotranspiration (Skov and Svenning 2004). It is a widely used measure that represents moisture availability for plant growth by relating precipitation to energy. A measure of theoretical solar radiation (mean and standard deviation) was calculated in ArcMap 10.2 using a model of clear sky insolation and exposure of different slopes (McCune and Keon 2002). The measure provides an estimate of potential annual direct incident radiation at each 1-km<sup>2</sup> grid cell.

Considering the study aims, extent and modelling resolution, measures of geodiversity (geomorphological, hydrological and geological richness) were compiled following Hjort and

Luoto (2010, 2012). Geomorphological richness was quantified using landform observations, GIS-based environmental variables and generalized additive modelling (Hjort and Luoto 2012), and measured as the number of landform types in each grid cell (a detailed description of the modelling of geomorphological richness is presented in Tukiainen et al 2016).

Hydrological richness was measured by summing the number of different hydrological feature types in a 1-km<sup>2</sup> grid cell, regardless of the number and cover of the specific features in the study grid cells. The following features were considered as hydrological feature types: aquifers (Finnish Environment Institute 2013b), wetlands (NLS 2012) and rivers, lakes and sea-areas (Finnish Environment Institute 2015). Respectively, ‘geological’ richness was measured by summing the number of different soil and rock types in a grid cell (together, rather than separate variables for soil and rock type richness). Rock types were determined using a digital bedrock map produced by the Geological Survey of Finland (GSF 2010a), in which bedrock types were classified by an expert into 16 genetically and geochemically distinct classes. Soil types were derived from a digital soil map produced by the Geological Survey of Finland (GSF 2010b), 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. In addition to the different measures of geodiversity, a measure of total geodiversity (i.e. georichness; Fig. 2) was computed by summing geological, geomorphological and hydrological richness values (following Hjort et al 2012). Though simple, this way of quantifying geodiversity follows the current standard in the geodiversity literature (a review of measures is presented in Pellitero et al 2015).

We employed analysis of principal coordinates of neighbour matrices (PCNMs; Borcard and Legendre 2002) to create spatial variables to use in our analyses. PCNMs are calculated from geographical distances between sites, and model spatial relationships among sites in

decreasing order of spatial scale. They were developed to account for induced spatial dependence between statistical units due to effects of external processes (Dray et al 2012, Peres-Neto and Legendre 2010), the basic idea being that even if spatial autocorrelation cannot be avoided, spatial structure can provide useful information. Thus we use them to account for unmeasured influences such as dispersal limitation. PCNMs belong to the model family of Moran's eigenvector maps, which are related to Moran's I (a measure of spatial autocorrelation). Eigenvectors with positive autocorrelation are searched for and used to describe spatial structures in a given dataset (Borcard and Legendre 2002). These eigenfunction-based procedures allow spatial analysis at different spatial scales and thus can address complex patterns of spatial variation. The first eigenvectors represent broad-scale spatial patterning of study units, while later ones (with smaller eigenvalues) represent finer-scale variation (Peres-Neto and Legendre 2010). The PCNMs are mutually orthogonal, linearly unrelated spatial variables, avoiding multicollinearity problems.

The following steps were followed to obtain PCNMs (see Borcard and Legendre 2002 for details): 1) calculation of a matrix of Euclidean geographic distances between grid cells based on their geographical centres; 2) construction of a truncated connectivity matrix ( $W$ ) according to the rule  $w_{ij} = d_{ij}$  if  $d_{ij} \leq t$  and  $w_{ij} = 4t$  if  $d_{ij} > t$ , where  $t$  is the maximum distance (minimum spanning tree which maintains all grid cells being connected); 3) principal coordinates analysis of the truncated distance matrix, extracting eigenvectors with positive autocorrelation. Significant variation accounted for by PCNMs may reflect environmental autocorrelation, dispersal limitation or historical effects on vascular plant richness (Dray et al 2012; Peres-Neto et al 2012). Separate PCNM analyses were run for grid cells in each of the three land-use intensity categories. Original PCNMs for each of the three land-use intensity categories yielded 88 spatial variables for low-human-impact areas (category 1), 107 for moderate human impact (category 2) and 54 for areas of high human impact (category 3).

Since the aim was to account for spatial autocorrelation and influences other than those measured by our explanatory variables, we only retained spatial variables that both (i) showed short-distance spatial autocorrelation and (ii) correlated as little as possible with the measured environmental variables. Thus, we only chose spatial variables that were uncorrelated (Spearman's rank  $P > 0.01$ ) with all the selected climate and geodiversity variables. This resulted in selection of 54 spatial variables (eigenvectors) for areas of low human impact, 89 for areas of moderate impact and 22 for areas of high human impact for the final analyses. PCNMs were constructed using the PCNM package in the R environment (Legendre et al 2013).

The selection of the climate and geodiversity variables for the analyses was made so that correlations (Spearman's rank-order correlation,  $r_s$ ) within the variable groups were  $< |0.75|$  (e.g. Aalto and Luoto 2014), in order to minimize collinearity problems. If  $r_s$  between two explanatory variables was  $> |0.75|$ , the one selected was determined by evaluating which correlated more strongly with species richness in conjunction with which was more theoretically relevant. Thus, in addition to all geodiversity measures, three climate variables (GDD, water balance and standard deviation of theoretical solar radiation) were chosen for further analysis (Table 1).

### *Statistical analysis*

The first study aim was to assess whether there is a hump-shaped relationship between geodiversity/biodiversity and the degree of human influence at the landscape-scale; for this, we used generalized additive modelling (GAM). More precisely, we used GAM-based response curves and the full data set ( $n=6191$ ) to graphically determine the diversity–hemeroby relationship. GAMs are particularly 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 (<http://r-project.org>). We calibrated the

GAMs using standard gam functions in the mgcv package and either a Gaussian or Poisson

305 (with a log link function) error distribution in the model fitting. The family and link function were determined based on exploration of residuals and smoothness selection scores

(generalized cross validation or unbiased risk estimator) of the models (Wood 2006, 2011).

To explore potential nonlinear relationships, the selected explanatory variables were fitted to the response (i.e. species richness or georichness) using a smoothing spline with the degrees

310 of freedom permitted to vary between one (i.e. straight-line relationship) and three.

We used GAM to compute both univariate and multivariate model-based response curves. In the univariate models, the hemeroby index was the only predictor variable. In the multivariate model, climate variables (GDD, water balance and standard deviation of theoretical solar radiation) were used as predictor variables in addition to the hemeroby index, 315 to control the effect of climate (i.e. broad-scale patterns) on the measures of biodiversity and geodiversity.

The second study question concerned the explanatory power of geodiversity variables, and how this varies with human land-use intensity. For this, the contribution of each variable group (climate, geodiversity and spatial variables) was analyzed using ordinary least-squares 320 regression-based variation partitioning (VP) (Borcard et al 1992). We used VP to measure the independent and shared contributions of the geodiversity, climate and spatial variable groups in explaining the spatial patterns of vascular plant species richness in landscapes of low, moderate and high human impact. Models were run in R. In the models, both linear and quadratic terms of the explanatory variables were used to capture the potential nonlinear 325 responses, except for spatial variables. The models were optimized using a backwards elimination approach (criterion:  $P < 0.05$ ).

We calibrated models using variables from (i) climate, (ii) geodiversity, (iii) spatial, (iv) climate and geodiversity, (v) climate and spatial, (vi) geodiversity and spatial groups, and (vii) variables from all three groups. The performance of each model was evaluated by using adjusted  $R^2$  coefficient of determination. Adjusted  $R^2$  provides unbiased estimation of the variation accounted for, and it is suitable in situations where the number of explanatory variables differs between the models (Guisan and Zimmermann 2000), as here. Based on the adjusted  $R^2$  values extracted from each of the seven ordinary least-squares regression models, we calculated the independent and shared fractions for the three explanatory variable groups, following the widely used procedure of Anderson and Gribble (1998).

## Results

Across the whole data set (6191 cells), the mean number of species was  $125 \pm 1.0$  standard error of the mean (SE) in areas of low human impact (category 1,  $n=2424$ ),  $206 \pm 0.9$  SE for moderate impact (category 2,  $n=3300$ ) and  $240 \pm 2.8$  SE in areas of high human impact (category 3,  $n=467$ ). The relationship between plant species richness and land-use intensity was positive and curvilinear (Fig. 3A). Species richness increased rapidly from low to moderately human-impacted environments (up to hemeroby index values of approximately 3.5). At higher hemeroby values, the increase in species richness levelled off. This pattern was evident in both the univariate model and the model including climate variables as covariates (multivariate model).

#Figure 3 approximately here#

The overall relationship between georichness and land-use intensity was very different to that for species richness (Fig. 3). In areas with moderate to high human impact, the

univariate and multivariate models showed similar trends, with a small increase in georichness from hemeroby values 3 to 5 and a larger decrease in georichness in the most human-impacted areas (hemeroby >5). In the least human-impacted environments (hemeroby index <3), there was a notable difference between the univariate and multivariate GAMs: the raw relationship (univariate model) was a strong negative relationship (georichness increasing with reduced human impact), but when controlling for climate (multivariate model) there was no relationship (Fig. 3B).

In the variation partitioning (VP), climate accounted for most of the explained variation, either on its own or as shared variation with geodiversity (Fig. 4). The biggest difference between the human-impact categories was that geodiversity had very low shared variation in areas of low human impact but high shared variation (with climate) in areas of moderate and high human impact. The overall contribution (unique plus shared variation) of geodiversity showed a similar trend, being highest at moderate human impact, for which its contribution was 20% of the variation in species richness. The unique contribution of geodiversity followed the opposite trend, but was small in all cases. The contribution of spatial variables was largest in areas of low human impact (4.7% unique; 9% overall) and minimal in areas of high human impact. The amount of undetermined variation varied between 46–61% in the models.

#Figure 4 approximately here#

Climate variables in the VP models were mainly non-linear (Table 2). Growing degree days, water balance and theoretical solar radiation had positive relationships with species richness, with strong positive trends for most of the cases (see Appendix 3 for the closer examination of the response shapes). All the geodiversity variables showed positive



relationships with species richness, except for geomorphological richness in areas of low human impact (Table 2; Appendix 3).

380 #Table 2 approximately here#

## Discussion

Georichness tended to be greatest in areas of low human impact and least in areas of very high human impact, in contrast to species richness (Fig. 3). Although natural factors and processes are the main determinants of the variability of abiotic features (e.g. Gray 2013), this is consistent with a negative effect of human action on geodiversity, which has been suggested by recent research, and is of concern with respect to the principle of conserving Nature's stage. For example, Gordon and Barron (2013) stated that human constructions limit the number of different geomorphological and hydrological formations, particularly in areas of high human impact such as urban areas. However, we did find a small increase in georichness with land-use intensity within the range of moderately impacted areas (around hemeroby classes 3 and 4; e.g. natural grasslands, coniferous and mixed forests, transitional woodland/shrub and pastures). This suggests that semi-natural environments can harbour high levels of geological, geomorphological and hydrological variability. This positive portion of the overall negative relationship between geodiversity and land-use intensity is probably due to the fact that agriculture is common in extensive river valleys and forestry in topographically variable landscapes; both of these landscape types harbour relatively high geodiversity (Serrano et al 2009; Hjort and Luoto 2010, 2012; Pellitero et al 2011; Garbarino et al 2013).

400 Vascular plant species richness increased from the most pristine to moderately human-impacted landscapes, after which the relationships levelled off (Fig. 3). Elsewhere, plant

species richness has also been found to be high in human-impacted environments, especially in mid-to-high latitudes (Kühn and Klotz 2006; von der Lippe and Kowarik 2008). That could be because human-induced environmental change tends to remove habitat for native species, while simultaneously producing new habitats for species adapted to disturbed and human-dominated environments, such as invasive plants (McKinney and Lockwood 1999; McKinney 2002, 2004). Additionally, humans tend to settle and prosper in species-rich areas, where climatic conditions are favourable and productivity is high (Ricketts and Imhoff 2003). Especially notable in our results (Fig. 3) was that species richness levelled off around hemeroby class 4, meaning that pastures, farmlands and areas of discontinuous and continuous urban fabric (for example) all seem to harbour approximately the same amount of species at the landscape scale.

With respect to our second main research question, the answer to whether measures of geodiversity account for the variation in plant species richness patterns best in areas of lowest human impact depends on how the variation shared with climate is interpreted (Fig. 4); and climate was modelled as being the dominant influence. The independent contribution of geodiversity to accounting for variation in plant species richness decreased from natural-state areas to strongly human-impacted environments (consistent with Hjort et al 2012; Lawler et al 2015), but was always small. In contrast, when the shared contributions are taken into account, the importance of geodiversity appeared to be highest in environments of moderate human impact, and also notably high in highly human-impacted environments. While rural areas are quite diverse in their geodiversity (as stated above), urban areas tend to be located near abiotic ecosystem services, such as geosystem services (e.g. construction materials and nutrients or minerals in the soil; Gray et al 2013) or water bodies (e.g. rivers and lakes), which increase abiotic diversity of human settlements. The shared contribution between climate and

geodiversity was high, which may indicate that climate and terrestrial abiotic diversity interact quite strongly in anthropogenic environments (cf. Räsänen et al 2016).

Our measures of geodiversity have been developed and used mainly in natural or semi-natural settings (Hjort et al 2012; Pereira et al 2013; Pellitero et al 2015). They only account  
 430 for geofeatures that tend to emerge naturally (geological, geomorphological and hydrological formations). However, urban areas are intensively modified by humans and have very high “non-natural geodiversity” – for example, buildings of all shapes and sizes and surfaces of different porosity (Erikstad 2013). In the future, it would be interesting to incorporate these human-modified “geofeatures” as part of abiotic diversity measures, and study whether this  
 435 type of geodiversity correlates with biodiversity in areas of varying human impact on the environment.

Climate variables had the largest contribution in accounting for variation in plant species richness for each of the three land-use categories. The independent contribution of climate to species richness was highest at natural-state environments, which is in line with  
 440 previous findings, where energy-related climatic variables have correlated strongly with species richness patterns (e.g. Kreft and Jezt 2007; Field et al 2009; Lawler et al 2015). In addition, climate contributed strongly in accounting for plant species richness in environments of high human impact. Temperatures in urban areas can be several degrees higher than in surroundings rural areas due to the urban heat island effect (Landsberg 1981), improving the  
 445 availability of energy for urban flora at high latitudes. Also higher CO<sub>2</sub> concentrations improve growth conditions of built environments (Ziska et al 2004). Additionally, in our data, most of the strongly human-impacted environments were located in southern parts of the country (Fig. 1), where annual temperature sum above 5°C is higher than in northern parts of the country (Pirinen et al 2012; Table 1).

450       The importance of pure spatial variables for plant species richness was always low and  
 decreased from weakly to strongly human-impacted environments. Furthermore, spatial  
 variables had little or no joint contribution with climate or geodiversity. This is mostly due to  
 our selection process of spatial variables, where we only selected spatial variables that were  
 not strongly correlated with climate or geodiversity variables. However, there was a slight  
 455   decreasing trend in the geographical structuring of climate variables from natural to strongly  
 human-impacted environments; i.e. the shared explanatory power of spatial and climate  
 variables decreased. This pattern might reflect the latitudinal and longitudinal gradients in  
 climate across Finland, which strongly affect plant species richness patterns (Pirinen et al  
 2012). The relatively small contributions of the spatial variables, suggest it is unlikely that  
 460   important spatially structured predictors (such as systematic dispersal limitation) are missing  
 from our models, even though the amount of unexplained variation was around 50%. Instead,  
 it is possible that we are missing factors that are not strongly spatially structured, which could  
 include various biological factors.

Many studies have reported the inherent linkages between geodiversity and biodiversity.  
 465   These links have been regarded as strong, particularly in environments of low human impact  
 (e.g. Hjort et al 2012). Our results suggest that a more nuanced perspective is appropriate.  
 According to our results, the unique contribution of geodiversity (over and above climate) to  
 accounting for variation in plant species richness was highest in areas of low human impact,  
 such as natural-state forests, inland marshes and peatbogs (cf. Räsänen et al 2016).  
 470   Independent of climate, geodiversity thus decreased in importance from small to negligible  
 towards highly human-impacted land use, whereas species richness was highest at  
 environments of urban and agricultural areas. Thus, the link between geodiversity and  
 biodiversity might not be as explicit in human-induced landscapes as in more natural-state  
 environments. However, the main contribution of geodiversity to modelling plant species

richness was indistinguishable from climate in our results, and the overall contribution was actually much higher in moderately and highly human-impacted areas. For future research, it is important to examine these relationships more closely; it is not yet clear whether ‘conserving Nature’s stage’ is a valid principle in human-impacted landscapes. Such research should span other geographical locations and spatial scales. Whether areas with currently high diversity of abiotic features are likely to support future biodiversity in changing climatic and biotic conditions (see Lawler et al 2015) remains an unresolved question.

## Conclusions

Better understanding of the connection between biodiversity and geodiversity along changing land-use gradients is important for developing sustainable measures to conserve biodiversity and landscapes under global change (Lindenmayer et al 2008; Matthews 2014; Lawler et al 2015), and to evaluate the extent to which ‘conserving Nature’s stage’ is a transferrable conservation principle. To address this, we examined the relationship between vascular plant diversity and geodiversity along a land-use gradient in sensitive high-latitude environments.

Firstly, we found that species richness was mainly positively correlated with human impact on the environment, but only up to a point, whereas the correlation between georichness and land-use intensity mostly showed the opposite trend. Thus, the notion of a unimodal, humped relationship between diversity measures and land-use intensity was partly supported, but mostly not supported, in our landscape-scale analysis. Secondly, the independent explanatory power of geodiversity on plant species richness was small throughout, but strongest in natural state environments. Most of the explanatory power of geodiversity was shared with climate (which had by far the greatest explanatory power), and, in contrast to the unique contribution, was lowest in natural-state environments. The correlation between geodiversity variables and species richness was predominantly positive across the gradient of land-use intensity. More

500 knowledge of relationships between geodiversity and biodiversity, and their variation along  
gradients of land-use intensity, is still needed to inform appropriate ways of conserving  
nature, especially under habitat fragmentation and rapid land-use change.

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## Tables

Table 1. Biodiversity, geodiversity and climate variables considered (n=6191, 1-km<sup>2</sup> resolution). From climate variables a total of three, indicated with \*, were selected for analysis, based on correlation analysis and theoretical considerations (see Methods section for further details). Total geodiversity (i.e. georichness) was used in producing response curves with generalized additive model (GAM), whereas separate measures of geological, hydrological and geomorphological richness were used in variation partitioning modelling. Spatial variables are not included in this table because the values of these variables are not interpretable.

Variable	Unit	Median [min to max]	Source
<b>BIODIVERSITY</b>			
Plant species richness	Number of vascular plant species	175 [32 to 431]	Atlas <sup>a</sup>
<b>GEODIVERSITY</b>			
Geological richness	Number of rock and soil types	4 [2 to 10]	GSF <sup>b</sup>
Hydrological richness	Number of hydrological feature types	2 [0 to 5]	NLS <sup>c</sup>
Geomorphological richness	Number of geomorphological feature types	6 [0 to 18]	GAM <sup>d</sup>
Total geodiversity (georichness)	Number of geological, hydrological and geomorphological feature types	12 [2 to 27]	GSF, NLS, GAM
<b>CLIMATE</b>			
Mean annual air temperature	°C	3.8 [-2.9 to 6.4]	FMI <sup>e</sup>

		1253.3 [245.8 to	
Growing degree days (>5°C)*	degree-days	1487.2]	FMI
Mean annual precipitation	mm	629.7 [409.4 to 756.7]	FMI
Potential evapotranspiration	mm year <sup>-1</sup>	346.4 [147.5 to 405.9]	FMI
Water balance*	mm year <sup>-1</sup>	299.2 [138.9 to 437.5]	FMI
Theoretical solar radiation (mean)	Mj cm <sup>-2</sup> year <sup>-1</sup>	0.5 [0.3 to 0.6]	DEM <sup>f</sup>
Theoretical solar radiation (std)*	Mj cm <sup>-2</sup> year <sup>-1</sup>	0.03 [<0.01 to 0.2]	DEM

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<sup>a</sup> Atlas of the Distribution of Vascular Plants in Finland

<sup>b</sup> Geological Survey of Finland.

<sup>c</sup> National Land Survey of Finland.

<sup>d</sup> Tukiainen et al (2016).

<sup>e</sup> Finnish Meteorological Institute. The climate variables are for the period 1981–2010.

<sup>f</sup> Digital Elevation Model.



Table 2. The linear (L) and quadratic (Q) terms of the explanatory variables selected from climate and geodiversity variable groups and used in the variation partitioning for modeling vascular plant species richness at environments of different human impact (low, moderate or high). The direction of the effect of predictor variables is indicated (+ = positive effect, - = negative effect) (see also Appendix 3).

	Low human impact	Moderate human impact	High human impact
CLIMATE			
Growing Degree Days	Q <sup>-+</sup>	Q <sup>-+</sup>	Q <sup>-+</sup>
Water Balance		Q <sup>-+</sup>	Q <sup>+−</sup>
Theoretical solar radiation std	Q <sup>+−</sup>	Q <sup>+−</sup>	L <sup>+</sup>
GEODIVERSITY			
Geological richness	L <sup>+</sup>	L <sup>+</sup>	L <sup>+</sup>
Hydrological richness	L <sup>+</sup>		
Geomorphological richness	Q <sup>+−</sup>	Q <sup>-+</sup>	Q <sup>-+</sup>

## Figure captions

Figure 1. Land use of Finland (A) and the location of sampled 1x1-km grid cells (467 grid cells in each land-use category) illustrated as circles 10 km in diameter (B) (for further details, see Methods). Land use is divided to three categories: areas of low, moderate and high human impact on the environment (same colour scheme for maps A and B). Land-cover classification is based on a hemeroby index (Walz and Stein 2014) which was computed using CORINE Land Cover 2006, tree stand age (Luke 2011) and protected area data (Finnish Environment Institute 2013a).

Figure 2. Land-use intensity (hemeroby), species richness and georichness across Finland (for details on the computations, see Methods). Coloured dots represent the grid cells studied (n=6191). The grey background includes a three-dimensional terrain view, based on a digital elevation model. Lakes and large rivers are shown in white. Appendix 1 provides a larger version of the figure.

Figure 3. Response curves with 95% confidence limits of vascular plant species richness (A) and georichness (B) in relation to the intensity of land use (hemeroby index). The response curves were obtained through generalized additive models (GAMs) using univariate (in blue) and multivariate (in red) models (the multivariate models include climate variables as well as hemeroby; see the text for further details). The univariate and multivariate GAMs accounted for 48.5% and 65.7% of the variation (adjusted  $R^2$ ) in species richness, respectively, and 16.4% and 40.3% of the variation in georichness.

Figure 4. Results of variation partitioning for environments of low (A), moderate (B) and high (C) human impact on the environment, in terms of proportions of variation accounted for (%) in the species richness data. Variation is partitioned into the independent contributions (a, b, c), the shared contributions (d, e, f, g) and the undetermined variation (U). Note that the shared variation can be negative in some cases because of suppressor variables or two strongly correlated predictors with strong, opposing effects on the response (Legendre and Legendre 2012). The climate group comprised growing degree days, water balance and standard deviation of theoretical solar radiation. Geodiversity variables were geological, hydrological and geomorphological richness. The spatial variable group included variables derived from Principal Component of Neighbour Matrices (PCNM) and there were 54 eigenvectors in areas of low human impact, 89 in areas of moderate and 22 in areas of high human impact.

## Figures

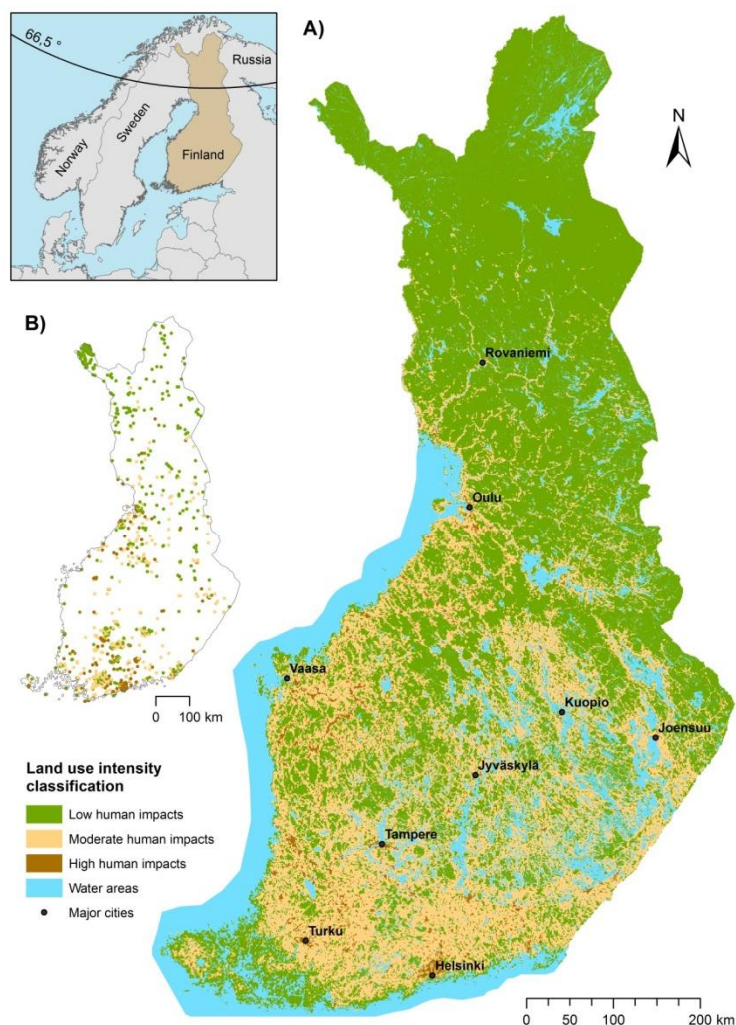


Figure 1. Land use of Finland (A) and the location of sampled 1x1-km grid cells (467 grid cells in each land-use category) illustrated as circles 10 km in diameter (B) (for further details, see Methods). Land use is divided to three categories: areas of low, moderate and high human impact on the environment (same colour scheme for maps A and B). Land-cover classification is based on a hemeroby index (Walz and Stein 2014) which was computed using CORINE Land Cover 2006, tree stand age (Luke 2011) and protected area data (Finnish Environment Institute 2013a).

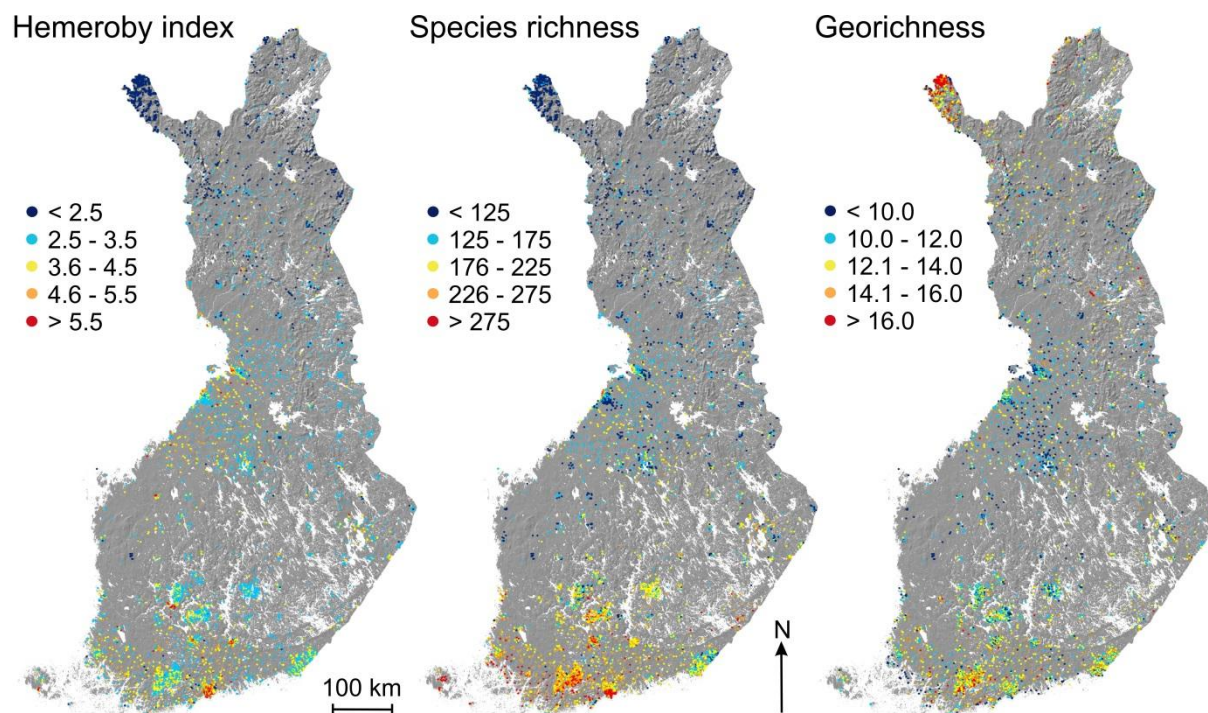


Figure 2. Land-use intensity (hemeroby), species richness and georichness across Finland (for details on the computations, see Methods). Coloured dots represent the grid cells studied ( $n=6191$ ). The grey background includes a three-dimensional terrain view, based on a digital elevation model. Lakes and large rivers are shown in white. Appendix 1 provides a larger version of the figure.

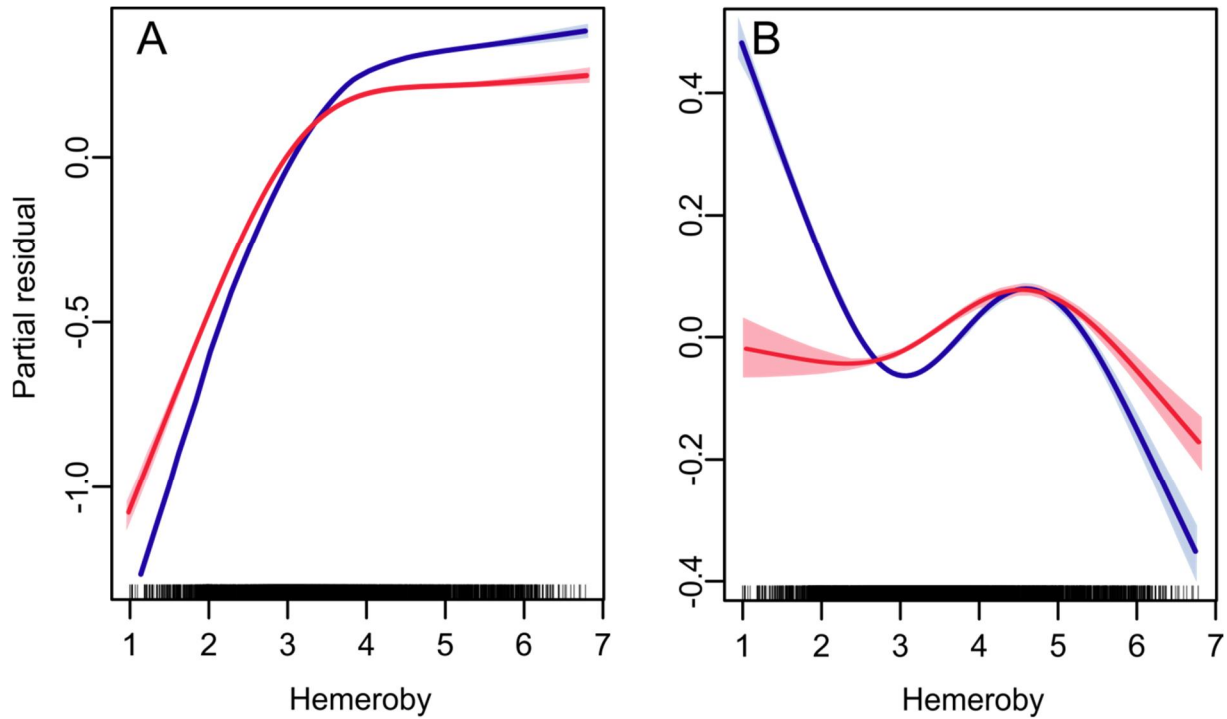


Figure 3. Response curves with 95% confidence limits of vascular plant species richness (A) and georichness (B) in relation to the intensity of land use (hemeroby index). The response curves were obtained through generalized additive models (GAMs) using univariate (in blue) and multivariate (in red) models (the multivariate models include climate variables as well as hemeroby; see text for further details). The univariate and multivariate GAMs accounted for 48.5% and 65.7% of the variation (adjusted  $R^2$ ) in species richness, respectively, and 16.4% and 40.3% of the variation in georichness.

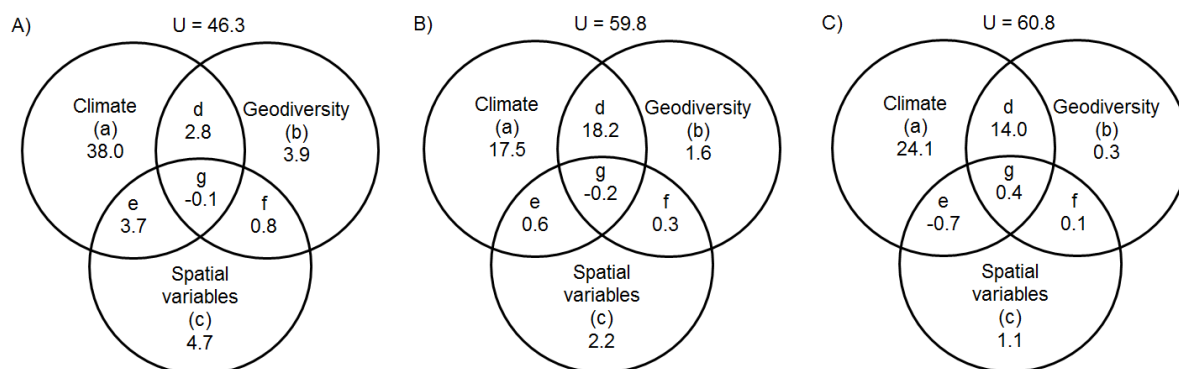


Figure 4. Results of variation partitioning for environments of low (A), moderate (B) and high (C) human impact on the environment, in terms of proportions of variation accounted for (%) in the species richness data. Variation is partitioned into the independent contributions (a, b, c), the shared contributions (d, e, f, g) and the undetermined variation (U). Note that the shared variation can be negative in some cases, because of suppressor variables or two strongly correlated predictors with strong, opposing effects on the response (Legendre and Legendre 2012). The climate group comprised growing degree days, water balance and standard deviation of theoretical solar radiation. Geodiversity variables were geological, hydrological and geomorphological richness. The spatial variable group included variables derived from Principal Component of Neighbour Matrices (PCNM) and there were 54 eigenvectors in areas of low human impact, 89 in areas of moderate and 22 in areas of high human impact.

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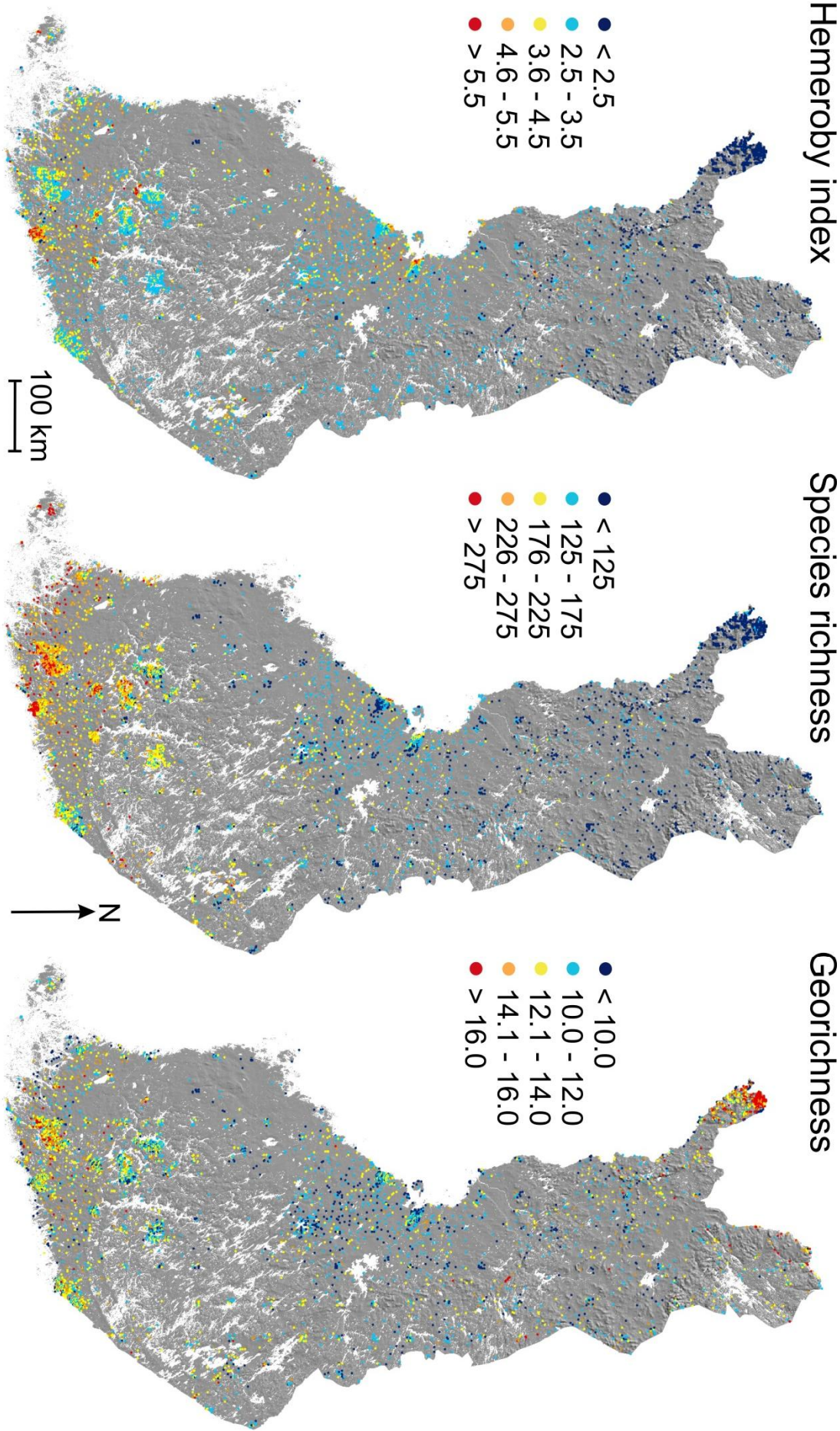
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**Appendix 1. A larger version of the Figure 2 representing the variation of land-use intensity (hemeroby), species richness and georichness across Finland**

Circular symbols represent studied grid cells (n=6191). A digital elevation model based three-dimensional terrain view is on the background. Lakes and largest river are shown in white.

For further details on the computation of hemeroby index and diversity measures, see the Methods section.



## Appendix 2. The assignment of CORINE Land Cover classes to hemeroby classification

The assignment of CORINE Land Cover classes (CLC) to degrees of hemeroby. In addition to CLC, also tree stand age data (Luke 2011) and protected area data (Finnish environment institute 2013a) is used for mixed and coniferous forest classes to make the classification more accurate.

Degree of hemeroby	CLC-code	
	(level 4)	CLC-class name (level 3)
1 ahemerobic (almost no human impacts)	3320	Bare rock
2 oligohemerobic (weak human impacts)	3111	Broad-leaved forests
	3112	Broad-leaved forests
	3121	Coniferous forest <sup>a</sup>
	3122	Coniferous forest <sup>a</sup>
	3123	Coniferous forest <sup>a</sup>
	3131	Mixed forest <sup>a</sup>
	3132	Mixed forest <sup>a</sup>
	3133	Mixed forest <sup>a</sup>
	3220	Moors and heathland
	3245	Transitional woodland/shrub
	3310	Beaches, dunes, and sand plains
	4111	Inland marshes
	4112	Inland marshes
	4121	Peatbogs
	4211	Salt marshes
	4212	Salt marshes
3 mesohemerobic (moderate human impacts)	3210	Natural grassland

	3121	Coniferous forest <sup>b</sup>
	3122	Coniferous forest <sup>b</sup>
	3123	Coniferous forest <sup>b</sup>
	3131	Mixed forest <sup>b</sup>
	3132	Mixed forest <sup>b</sup>
	3133	Mixed forest <sup>b</sup>
	3241	Transitional woodland/shrub
	3242	Transitional woodland/shrub
	3243	Transitional woodland/shrub
	3244	Transitional woodland/shrub
	3247	Transitional woodland/shrub
4 $\beta$ -euhemerobic (moderate-strong human impacts)	2310	Pastures
5 $\alpha$ -euhemerobic (strong human impacts)	1421	Sport and leisure facilities
	1422	Sport and leisure facilities
	1423	Sport and leisure facilities
	1424	Sport and leisure facilities
	2111	Non-irrigated arable land
	2112	Non-irrigated arable land
	2220	Fruit trees and berry plantations
6 polyhemerobic (very strong human impacts)	1120	Discontinuous urban fabric
	1310	Mineral extraction sites
	1320	Dump sites
	1330	Construction sites
7 metahemerobic (excessively strong human impacts)	1110	Continuous urban fabric
	1210	Industrial or commercial units

1220	Road and rail networks and associated land
1230	Port areas
1240	Airports

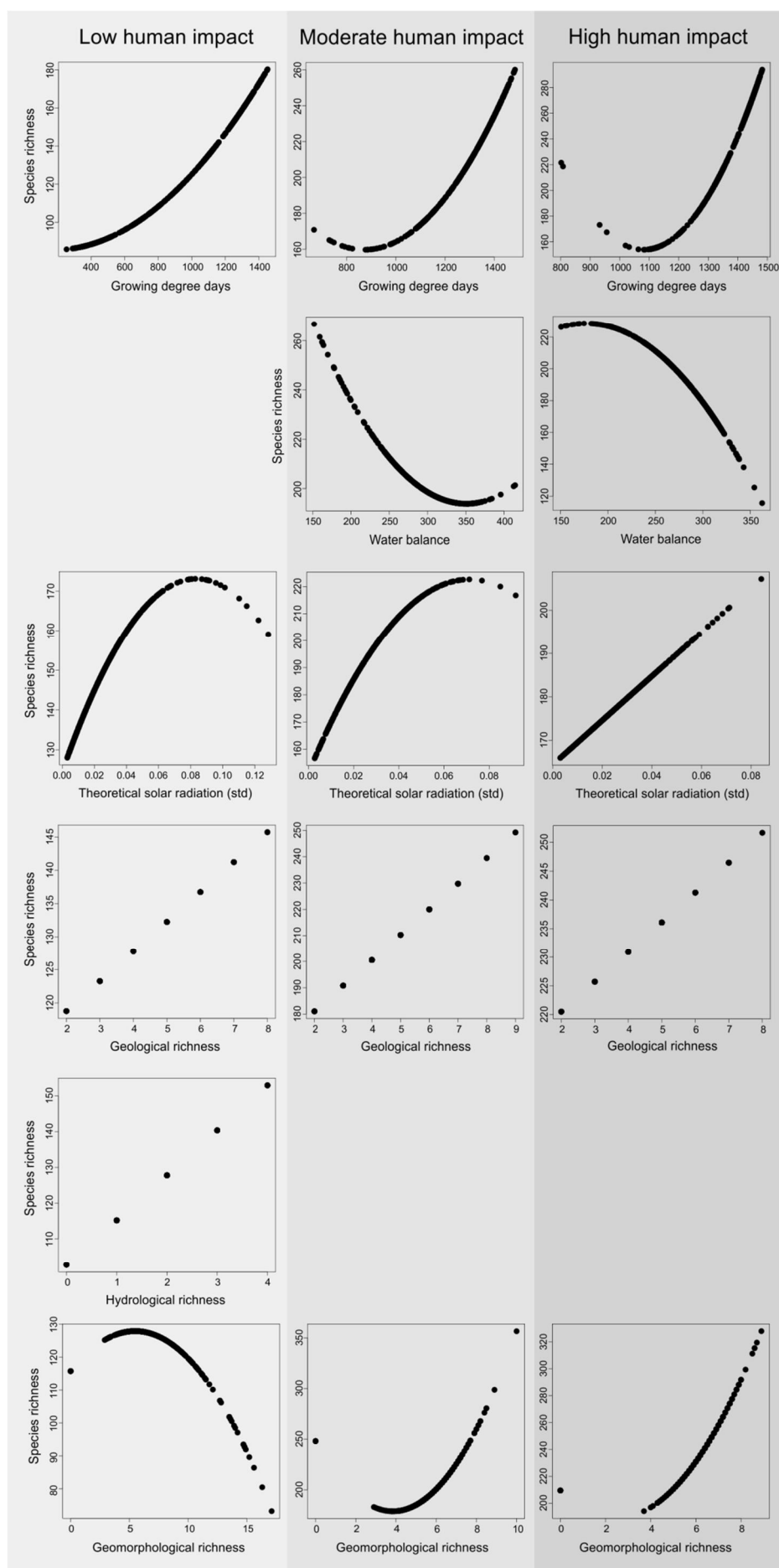
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<sup>a</sup> If the age of the tree stand is  $\geq 80$  years or if located in protected area.

<sup>b</sup> If the age of the tree stand is  $< 80$  years

### **Appendix 3. The relationship between predicted species richness and environmental variables**

The relationship between predicted species richness and environmental variables based on ordinary least-squares regression models (see Table 2 and the text for further details). To obtain univariate response profile, the remaining model variables were fixed at the median value (Brenning and Trombotto 2006).



## References:

- Brenning A, Trombotto D (2006) Logistic regression modeling of rock glacier and glacier distribution: topographic and climatic controls in the semi-arid Andes. *Geomorphology*, 81:141-154