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Multi-scale relationship between geodiversity and biodiversity across high-latitude environments: implications for nature conservation

Helena Tukiainen

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Abstract

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Keywords: geodiversity, biodiversity, landform, geofeature, boreal region, GIS, statistical modelling, vascular plants, threatened species, nature conservation

The natural diversity of Earth consists of two main elements: the diversity of biotic nature (biodiversity) and the diversity of abiotic nature (geodiversity). Their relationship is theoretically strong but insufficiently studied. A conservation principle called Conserving Nature´s Stage (CNS) states that geodiversity (e.g. data on geological, geomorphological and hydrological richness) could be used as a coarse filter strategy for conserving biodiversity in changing environmental conditions. It is based on an idea that areas where geodiversity is high are capable of supporting high biodiversity, because organisms depend on the abiotic "stage" on which they exist. The capability of present conservation actions to protect and sustain biodiversity in the face of global change is under debate, and CNS is proposed as one complementary solution to this issue. There is an urgent need for studies that examine the relationship between geo- and biodiversity to assess the possibilities of CNS for nature conservation.

In this thesis, I explored the potentiality of how geodiversity information can be used in assessing biodiversity by examining their relationship in different areas, at different spatial scales and with different measures. This thesis consists of three studies: (1) a study where the importance of geodiversity, topographical and climatic variables to threatened species diversity and rarity was analysed, (2) a study where geodiversity and vascular plant species richness were examined at different land-use intensity (hemeroby) levels, and (3) a study where landforms were evaluated based on their vascular plant diversity. My most important goal was to determine how landforms and landscape-scale geodiversity (i.e. variables for which the geological, geomorphological and hydrological feature richness are accounted) are related to biodiversity (i.e. the species diversity and rarity of vascular plants and other taxa).

The results highlighted the overall positive relationships between geo- and biodiversity in high-latitude environments. Geodiversity variables had consistent positive effects on threatened species richness, especially for threatened vascular plants. Of geodiversity variables, geomorphological richness was the most important predictor for most taxa, indicating that the landscape-scale variability of landforms plays an important role in determining threatened species richness patterns. Independent geodiversity contributions for vascular plant species richness were highest in pristine environments throughout Finland, and geodiversity land-use intensity relationships were mainly negative. Landforms were, in general, more diverse than control sites and there was notable variation in plant species diversity between different landforms. Gullies and river shores

were the most diverse landforms at alpha and gamma diversity levels, whereas aapa mires were taxonomically the most unique (i.e. they had the highest beta diversity).

To conclude, geodiversity added explanatory power for biodiversity models and accounted uniquely for richness patterns for both common and threatened species. Geodiversity variables that take into account the variation in soil, rock, geomorphology and hydrology have importance for biological communities at high latitudes and should be incorporated into conservation management and planning. This reinforces recent arguments that CNS is an important and valid principle in conservation. More knowledge on the relationship between geodiversity and biodiversity is still needed, encompassing different biomes and geographical extents to inform appropriate ways of conserving nature, especially in the context of ongoing global change.

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List of Original publications

This thesis is a summary of the following articles, which are referred to in the text by their Roman numerals:

I Tukiainen, H., Bailey, J.J., Field, R., Kangas, K. & J. Hjort (2017). Combining geodiversity with climate and topography to account for threatened species richness. *Conservation Biology* 31: 364-375.

II Tukiainen, H., Alahuhta, J., Field, R., Ala-Hulkko, T., Lampinen, R. & J. Hjort (2017). Spatial relationship between biodiversity and geodiversity across a gradient of land-use intensity in high-latitude landscapes. *Landscape Ecology* 32: 1049-1063.

III Tukiainen, H., Kiuttu, M., Kalliola, R., Alahuhta, J. & J. Hjort (2019). Landforms contribute to plant biodiversity at alpha, beta and gamma levels. *Journal of Biogeography*, accepted.

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Author´s contributions:

I All authors conceived the research. All authors except RF amassed the data. JJB and HT did the main analyses and wrote the text with major contributions from RF and JH. All authors commented on and edited the text.

II HT, TA, JH and JA conceived the ideas. HT, TA, JA and RL collected the data and HT, JA and JH analysed the data. HT wrote the text with contributions from JA, RF and JH. All authors commented on and edited the text.

III MK, JH and HT conceived the ideas. HT, MK, JH and JA collected and analysed the data. HT led the writing with contributions from MK. All authors commented on and edited the text.

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1 Introduction

Biodiversity is declining rapidly due to increasing human pressure and global climatic and land-use change. Compiling evidence for a theoretically strong, yet insufficiently explored linkage between geodiversity and biodiversity is of high importance in the face of these global changes. It is proposed that geodiversity could be used as a cost-effective coarse-filter surrogate for predicting biodiversity patterns (Conserving Nature´s Stage, CNS framework). If strong evidence for this framework is found, the areas of expected high climate resilience could be identified with geodiversity information, without complex modelling of climate and individual species´ responses (Beier *et al.* 2015). Thus, it is valuable to analyse the extent to which this kind of novel abiotic data can be used in biodiversity studies and in nature conservation. In this study, the relationship between geodiversity and biodiversity is analysed with multiple datasets, up-to-date quantitative methods and several spatial scales in boreal and arctic environments.

1.1 Biodiversity

Biological diversity, or biodiversity, is defined by the United Nations in the Convention on Biological Diversity as *"the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems"* (CBD 1992; Figure 1). Despite the broad interpretation, especially the spatial patterns in species diversity have been in the focus of ecological and biogeographical studies, and a major goal in ecology has been to model and understand the spatial patterns of species distributions (Guisan & Zimmerman 2000; Lomolino *et al.* 2010). Vascular plants are a commonly studied taxonomic group and typically their distribution and diversity patterns are strongly correlated with climatic variables and topographical heterogeneity (Field *et al.* 2009), whereas the effects of other abiotic conditions are less known, especially for rare species in other taxonomic groups (e.g. Virkkala *et al.* 2005; Anderson & Ferree 2010).

1.1.1 Measuring biodiversity

Understanding spatial patterns of biodiversity is essential for nature conservation and for the management of ecosystem services (Lomolino *et al.* 2010; Hanski *et al.* 2012) (Figure 1). Ecologists have devoted considerable effort to the explanation of patterns of diversity in ecological systems (Peet 1974). Biological diversity consists of two principal components: richness, or the variety of species, and evenness, or the way in which the individuals are distributed among those species (their relative abundance) (Ibáñez *et al.*

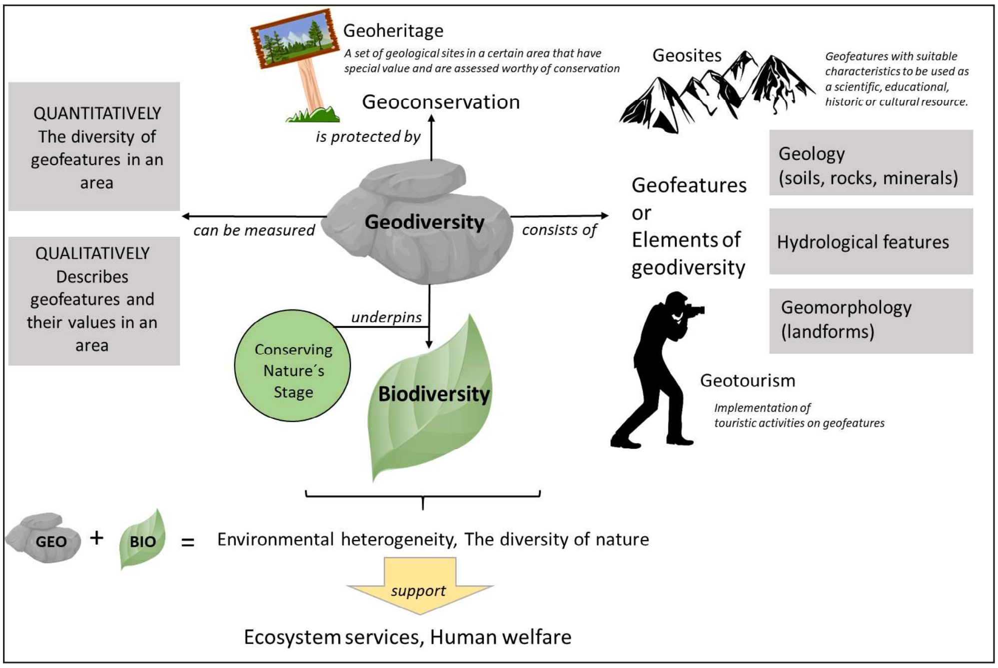

Figure 1. Conceptual framework of geodiversity (the abiotic richness of the earth's surface) and biodiversity (biological diversity), binding the most important concepts related to this study (ideas from Brilha *et al.*, 2018).

1995). The most commonly used, and the simplest measure of biodiversity is species richness, or the number of different species within the study unit (Purvis & Hector 2000; Field *et al.* 2009; Magurran & Dornelas 2010). In addition, several heterogeneity indices have been developed in attempt to combine measures of richness and abundance.

Foremost among these are Simpson´s diversity and Shannon´s (or Shannon-Weaver) diversity indices which differ both in their theoretical foundation and interpretation (Hill 1973; Magurran 2004). The Simpson index is one of the most commonly used diversity measures available and the first of the heterogeneity indices used in ecology (Peet 1974; Magurran 2004). It measures the probability that two individuals selected at random from a sample will belong to the same species (Peet 1974). However, it varies inversely with heterogeneity meaning that as the value of the index increases, diversity decreases. Thus, the reciprocal of Simpson´s index is commonly used. In this form, the index can be interpreted as the number of equally common species required to produce the same heterogeneity as observed in the sample (Hill 1973; Peet 1974; Magurran 2004). Shannon`s diversity index is based on information theory and it represents the uncertainty about the identity of an unknown individual, or how unlikely it is to choose two members of the same factor from a group of multiple factors (Shannon 1948; Peet 1974). For instance, the more vascular plant species there are in an area and the more even their representation is, the greater the uncertainty and hence the greater the diversity (Ibáñez *et al.* 1995).

These three measures (species richness, Simpson index and Shannon´s diversity index) of biodiversity have strong relationships but are not interchangeable. Compound indices are often preferred over species richness when ranking sites by their level of diversity is the primary goal (Magurran & Dornelas 2010). In contrast, simple biodiversity indices, like species richness, could be more effective in cases where the objective is to detect effects of external factors on diversity (Magurran & Dornelas 2010). In addition, biodiversity can be measured with focus on rarity, since one of the key issues in conservation planning is to identify a group of sites that collectively represent all species in a small area (Pressey *et al.* 1993). Rarity is best viewed as a continuous variable using a single rarity metric (Magurran 2004). Rarity-weighted richness (RWR) is a simple, reliable way to identify sites that represent the largest number of species within a given number of sites and a noteworthy alternative to the more complicated heuristic algorithms that are commonly used for this purpose (Albuquerque & Beier 2015).

Biodiversity is commonly observed at three spatial scales: alpha, beta and gamma. Alpha, or within-site diversity, is the mean species diversity at the local, within-site scale. Beta, or between-community diversity, is the difference of species between sites, or the change in species composition over a relatively small distance. Gamma, or between-region diversity, is the total species diversity at the regional or landscape scale (Whittaker 1960; Lomolino *et al.* 2010; Tuomisto 2010). It is possible to measure alpha and gamma diversity with the same measures, e.g. with species richness or diversity indices such as Simpson´s or Shannon´s measures (Whittaker 1960). The definitions and means to compute beta diversity have been widely argued (Tuomisto 2010). It is generally acknowledged that beta diversity should be studied with respect to gradients (Whittaker 1960), but it is usually understood as a measure of general heterogeneity (Tuomisto 2010). Two distinct processes shape communities and their differences: species substitution and species loss or gain. The substitution of species on one site by different species on another site results in species replacement, while species loss or gain results in richness differences between sites. Thus, total beta diversity is the sum of species replacement and species richness differences (Carvalho *et al.* 2012; Cardoso *et al.* 2015).

1.1.2 Biodiversity in conservation and legislation

Research on biodiversity is the cornerstone of conservation biology and natural reserve design (Shaffer 1990). In short, the goal of biodiversity conservation is maintaining the diversity of species (Lomolino *et al.* 2010), and the criteria most frequently used in conservation assessments are species richness and endemism (Lindemayer & Burgman 2005; Ibáñez *et al.* 2012). The knowledge on global change and its consequences (such as the increasing extinction of species) has awakened great interest in appraising and preserving biodiversity. Numerous studies have focused on how global change, especially climate change, effects future biodiversity and how conservation practitioners should react to the changes (e.g. Hannah *et al.* 2002; Pressey *et al.* 2007; Bellard *et al.* 2012; Vilmi *et al.* 2017).

The growing human population presents many threats, such as land conversion, habitat destruction, pollution, climate change and overexploitation, which places organisms under enormous pressure (Mantyka-Pringle *et al.* 2012; Pacifici *et al.* 2015; Steinbauer *et al.* 2018). One of the greatest threats to biodiversity is land-use change which modifies natural and semi-natural environments to more anthropogenic landscapes (Vitousek *et al.* 1997). Only a quarter of land on Earth is substantively free of the impacts of human activities today, and the proportion is projected to decline to just one-tenth by 2050 (WWF, 2018). Thus, global biodiversity conservation depends increasingly on maintaining biodiversity in human-dominated landscapes (Fahrig *et al.* 2011). In semi-natural landscapes, land use has not radically changed biological and abiotic conditions, whereas in urban and intensive agricultural areas these characteristics have been severely modified, fundamentally shifting the whole ecosystem (Brown *et al.* 2005; Newbold *et al.* 2015). Biodiversity responses to human impact can vary extensively, but in areas where human disturbance is not (yet) extreme, such as agricultural or semi-urban environments, favourable environmental conditions for different species increase as spatial heterogeneity increases. In addition, the introduction of alien species might affect positively on species number in rural and urban environments (Landsberg 1981; McKinney 2008).

The projected influences of climate change have negative impacts on biodiversity and ecosystems, including species loss and extinction (Allen *et al.* 2018). High-latitude ecosystems are especially sensitive to climatic warming because of their marginal locations and because projected rises in temperatures increase poleward (Meltofte *et al.* 2013; Allen *et al.* 2018). Ecological changes driven by environmental change have already occurred in Arctic areas, and vegetation responses to global warming may be complex (Post *et al.* 2009). The biodiversity of Europe is in continuous strong decline, especially in terms of species diversity. For example, of the assessed species living only in Europe and Central Asia, almost one third are threatened (IPBES 2018). Globally, there are over 93,500 threatened species on the International Union for Conservation of Nature (IUCN) Red List (Vié *et al.* 2009). The current estimated number of species in Finland is at least 45,000, of which 10.5% are classified as threatened and of which the majority lives in forests, rural biotopes and other cultural habitats (Rassi *et al.* 2010).

There are numerous global and international acts and documents that are concentrated on biodiversity conservation. Probably the most significant one is the Convention on Biological Diversity (CBD). It was an outcome of the United Nations Environment and Development Conference in Rio de Janeiro in 1992 where the conservation of biodiversity was approved as an essential part of sustainable development (CBD 1992). Today, many international organizations also work to promote the objectives of the CBD, including IUCN, and the United Nations Environment Programme (UNEP). At the European level, the most important nature conservation instruments and means of conservation are the Convention on the Conservation of European Wildlife and Natural Habitats (Council of

Europe 1979), European Union directives (e.g. the Habitats Directive, the Birds Directive) and Natura 2000 protected area network. The European Union Biodiversity strategy up to 2020 aims to halt the loss of biodiversity and ecosystem services in the EU and help to stop global biodiversity loss by 2020 (EU 2011). In Nordic countries, there has been broad cooperation in the field of biodiversity conservation under the Nordic Council of Ministers since the late 1960s (Haapanen 2005). Furthermore, Polar nature conservation is the focus of many programmes of the Arctic Council (e.g. Conservation of the Arctic Flora and Fauna, CAFF) (Meltofte *et al.* 2013).

Today, Finland is a party to all global or relevant regional and international conventions where the conservation and sustainable use of biodiversity are significant objectives, such as CBD (Ahokumpu *et al.* 2009; Metsähallitus 2016). The first Nature Conservation Act was passed in 1923 and the most recent major update of the law was in 1996. According to the law, the aim of nature conservation is to ensure nature's diversity by ensuring that the favourable conservation status of different natural habitat types and native species is maintained or restored (Nature Conservation Act 1096/1996). The National Strategy for the Conservation and Sustainable Use of Biodiversity was approved by a Government resolution in 2012 and the complementary Action Plan 2013–2020 in the following year (ME 2012). The main objective of the strategy is to halt biodiversity loss in Finland by 2020. In addition, since the 1930s, Finland has been systematically building a comprehensive and diverse protected area network which consist of 803 statutory nature reserves of which 40 are national parks (Haapanen 2005; Metsähallitus 2016). The network of protected areas must primarily preserve *"areas of natural habitat, particularly habitat types characteristic of the Finnish landscape, and habitats, land forms, and features that are endangered"* (Metsähallitus 2016).

1.2 Geodiversity

Geodiversity constitutes a fundamental part of the earth system and is broadly defined as the variability of abiotic nature, or the abiotic richness of the earth's surface (Gray 2013). The concept of geodiversity was first introduced in 1993, when a number of geoscientists independently started using the term (Sharples 1995; Brilha *et al.* 2018). This was probably due to the CBD that was agreed at the Rio Earth Summit in 1992 and the word biodiversity came into general use. Geoscientists recognized that they study diverse phenomena on our planet, and developed an equivalent concept for biodiversity (Brilha *et al.* 2018; Gray 2018). Subsequently, the term geodiversity has been increasingly referred to and is now internationally recognized.

Although the term geodiversity is widely recognized, there is a multiplicity of concepts and definitions concerning the diversity of abiotic nature in scientific literature (Zwoliński *et al.* 2018). Probably the most commonly used geodiversity definition is by Gray (2013), who defined it as *"the natural range (diversity) of geological (rocks, minerals, fossils), geomorphological* *(landforms, topography, physical processes), soil and hydrological features. It includes their assemblages, structures, systems and contributions to landscapes."* Furthermore, it is recognized that geodiversity comprises geofeatures or elements of geodiversity, which are, for instance, the individual landforms that constitute the abiotic landscape, as well as minerals, fossils, rocks, soils and active geological and geomorphological processes (Brilha 2016, 2018; Bailey *et al.* 2017). In this thesis, geodiversity is more precisely defined as the diversity of geological (rock and soil), geomorphological and hydrological features (Hjort & Luoto 2010; Hjort *et al.* 2012; Pellitero *et al.* 2015; Figure 1). This definition of geodiversity is amongst the most specific ones in the context of the wider literature, since it omits crude topographical Digital elevation model (DEM) -based measures (such as mean slope or elevational range) and climatic data. DEM-based and climatic measures have been widely used as abiotic correlates or predictors of species richness (Barthlott *et al.* 2007; Stein *et al.* 2014; Antonelli *et al.* 2018) as well as they are often used as indicators of geodiversity (e.g. Benito-Calvo *et al.* 2009; Parks & Mulligan 2010; Pellitero *et al.* 2015). I omitted them to make a conceptual distinction and to study only the explicit geodiversity measures (see also Hjort *et al.* 2012; Bailey *et al.* 2018).

1.2.1 Measuring geodiversity

Geodiversity has been quantified in a multiplicity of ways in the scientific literature, both qualitatively and quantitatively (e.g. Ruban 2010; Seijmonsbergen *et al.* 2018; Zwoliński *et al.* 2018; Figure 1). Qualitative assessments of geodiversity are usually descriptive and are based on the knowledge of experts. Quantitative methods, which are used also in this thesis, are more common, and are derived from field instrumental measurements, numerical calculations or GIS (Geographic Information System) analyses of raw data (see the review by Zwoliński, Najwer & Giardino 2018 for further details and examples). For instance, several types of geodiversity indices have been developed to describe the geodiversity of an area. Ruban (2010) introduced several indices which were based on geosite types and their importance. Serrano and Ruiz-Flaño (2007) calculated a geodiversity index as the number of different physical elements in a grid cell times a coefficient of roughness, divided by the natural logarithm of the surface area or unit. This is the most popular method to calculate geodiversity index, later improved by others (Pellitero *et al.* 2015; Zwoliński *et al.* 2018). Amongst the most recently developed indices is the one by Seijmonsbergen *et al.* (2018), who generated a geodiversity index -based map, which is composed of various sub-indices of geodiversity (from tectonic, geological, hydrological, LiDAR and DEM-based data).

The term geodiversity is flexible and useful in describing the complexity of nature but it is not the only concept that refers to the variety in abiotic nature. Concepts like geomorphodiversity and geomorphosites have been introduced to make specifications within the wider concept (Reynard & Panizza 2005; Reynard 2009; Erikstad 2013).

Furthermore, pedodiversity, or the diversity of soils, has gained attention and the relationship between pedodiversity, lithological diversity and landform diversity has been demonstrated in many environments (Ibáñez *et al.* 1995, 2012; Antonelli *et al.* 2018). The term land facets refers to landscape units with uniform topographical and soil attributes. Several studies describe the correlation between land facets and current distribution of species in several taxa, such as vegetation, birds and beetles (Wessels *et al.* 1999; Beier & Brost 2010). In a wider scope, spatial environmental heterogeneity has been determined as an umbrella term for all terms relating to spatial complexity, diversity, structure, or heterogeneity in the environment (Stein & Kreft 2014; Stein *et al.* 2014). It covers both biotic (land-cover and vegetation) and abiotic (climatic, soil and topographical) environmental heterogeneity. In a meta-analysis based on 192 studies, elevation range was the most frequent measure of environmental heterogeneity, whereas relatively few studies concentrated on climate or soil (Stein & Kreft 2014).

1.2.2 Geodiversity in conservation and legislation

Geodiversity can have significance and value in scientific and educational interests, as well as intrinsic, cultural, aesthetic, economic and functional (for both physical and ecological processes) values that provide or contribute to a range of ecosystem services (Gray 2013; Alahuhta *et al.* 2018; Gordon 2018; Seijmonsbergen *et al.* 2018). Geodiversity provides natural capital, or abiotic ecosystem services, which have been exploited by society over many millennia (Gray *et al.* 2013). Some of this capital is renewable (e.g. freshwater resources) and some non-renewable (e.g. minerals and oil). Ecosystem services provided by abiotic nature contain benefits from the three main categories (provisioning, regulation & maintenance, and cultural, see Haines-Young & Potschin 2018). They are divided to extractable and non-extractable natural resources (MA 2005; Brilha *et al.* 2018; Gray 2018). For instance, the *in situ* occurrence of geodiversity elements with suitable characteristics to be used e.g. as a scientific resource is known as geosites (Brilha *et al.* 2018; Figure 1). Geosites are features that have remarkable value from a geoheritage perspective (i.e. human recognition of the value is high) but their georichness (number of abiotic features) is not necessarily high (Hjort & Luoto 2010; Pellitero *et al.* 2015).

Geodiversity is dynamic and still changing, both due to natural and human-induced reasons (Goudie & Viles 2016). Threats to geodiversity are the result of natural processes and human-induced change, such as climate change, land-use change and sea-level rise (Gray 2013). For instance, weathering and erosion shapes mountains, hills and cliffs. Furthermore, sand is one of the most extracted materials worldwide, which is putting a strain on limited sand deposits and formations, degrading both geo- and biodiversity at the extraction areas (Torres *et al.* 2017). Geodiversity, as with the rest of our natural environment, needs to be cared for and carefully managed.

Geoconservation, or geodiversity conservation, aims at the identification, protection and management of valuable elements of geodiversity (Brilha 2016). Geoheritage, or a set of geological sites in a certain area that have special value, is that part of geodiversity that is assessed as worthy of geoconservation (Gray 2018; Reynard & Brilha 2018; Figure 1). Geodiversity is still quite seldom referenced in predominant environmental law and policy (Comer *et al.* 2015; Lawler *et al.* 2015), with some exceptions, such as in Spain (Spanish 47/2007 Law on Natural Heritage). However, influential international organizations are gradually starting to incorporate aspects of geodiversity into their strategies. For instance, The Common International Classification of Ecosystem Services (CICES) has considered abiotic ecosystem outputs more widely in their most recent classification (Haines-Young & Potschin, 2018). Geoconservation at the global level is represented by two UNESCO (United Nations Educational, Scientific and Cultural Organization) site networks: World Heritage sites and Global Geoparks. The Global Geoparks network consist of 140 Geoparks in 38 countries that have geoheritage of international significance (McKeever *et al.* 2010; Henriques & Brilha 2017).

IUCN, which has traditionally been focused on bioconservation, has today a Geoheritage Specialist Group whose purpose is to facilitate geoconservation. GEOBON (Group on Earth Observations Biodiversity Observation Network) has established an ecosystem structure working group where the condition of structural components of ecosystems, that lead to and maintain biodiversity characteristics, are the focus. In Fennoscandia, the Nordic Council of Ministers published a report introducing geodiversity (geological and geomorphological diversity) in the Nordic countries and makes recommendations on the use and management of geodiversity (Johansson 2000). There are also national-level initiatives, such as the United Kingdom Geodiversity Action Plan, which sets out a framework for geodiversity action across the whole UK. In Finland, the environmental administration has inventoried and evaluated geological formations (valuable eskers, rock sites, small-scale sites in bedrock, moraine formations and aeolian and shore deposits which are valuable in terms of nature and landscape conservation). The Finnish protected area network aims, among other things, at preserving geological and geomorphological features and especially features that are rare or declining as a consequence of human activity (Metsähallitus 2016).

1.3 Linking geodiversity and biodiversity

Geodiversity and the way it influences landscapes is fundamental to the distribution and diversity of habitats and species. Over geological time scales, biodiversity has been strongly driven by abiotic factors and long-term landscape evolution (Hoorn *et al.* 2010; Gill *et al.* 2015). Geodiversity has been recognized as a key driver of biodiversity and species distribution patterns, but it has been a slow process to consider it as a way to prioritize areas for biological conservation (Beier *et al.* 2015; Comer *et al.* 2015). Based on recent findings (e.g. Hjort *et al.* 2012; Gordon & Barron 2013; Räsänen *et al.* 2016), geodiversity accounts for species richness, especially in areas where human impact is not high.

It is proposed that the relationship between geo- and biodiversity is strongest at landscape- to region-scale (intermediate) spatial extents, whereas climate dominates species patterns at larger extents and biotic interactions often dominate at local extents (Field *et al.* 2009; Stein *et al.* 2014; Lawler *et al.* 2015). Species turnover and allopatric speciation should be important especially at larger (intermediate) spatial scales, which promote positive geodiversity-species richness patterns (Stein *et al.* 2014). On the other hand, on a local scale, landforms sustain variable conditions in their soil moisture, microclimate and microtopography, creating heterogeneous niche-space which promotes biological diversity (Lundholm 2009; Shroder 2013).

1.3.1 Conserving Nature´s Stage framework

Protected area design has been largely based on an assumption of relatively static biodiversity (Pressey *et al.* 2007). Rather than focusing on short-term preservation of current species and their composition, the focus of conservation and protected area design should be in planning for future environmental change with a main interest in integrity of ecological and evolutionary processes and maintaining species composition in the long term (Bennett *et al.* 2009). The CNS (Conserving Nature´s Stage) framework has been developed to be put forward as an important conservation principle stating that geodiversity could be used as a coarse filter strategy for conserving biodiversity (Beier *et al.* 2015; Figure 1). It is based on the idea that geodiversity supports habitat heterogeneity which arises, for instance, from the characteristics of the physical substrate, topographical effects on microclimate and disturbance regimes from continual and episodic processes (Gordon 2018). Most species depend on this abiotic "stage" on which they exist, and habitat diversity and species richness are generally greater in areas where abiotic heterogeneity is high (Lundholm 2009; Anderson & Ferree 2010). The wider the gradient of environmental conditions, the more niche space there is for species and the higher total biodiversity the environment can support (Comer *et al.* 2015). When a wide array of geophysical settings with associated ecological processes is conserved, it not only preserves the places occupied by species today, but also preserves places that may be occupied in the future, as the climate changes and ecosystems transform (Comer *et al.* 2015). Therefore, CNS targets the areas that are high in geodiversity and thus have a high probability of harbouring high biodiversity and sustaining key abiotic and ecological processes in the unpredictable future (Lawler *et al.* 2015; Gordon 2018).

The first coarse-filter approach to conservation was used by The Nature Conservancy in the United States, which aimed to conserve examples of each vegetation community, under the assumption that most species would be protected using this filter (The Nature Conservancy 1982; Beier *et al.* 2015). At the end of 1980´s, Hunter *et al.* (1988) argued that physical environments would make better surrogates for conservation planning than present vegetation communities in the face of climate change. This probably was the first time conserving geodiversity was proposed as a surrogate for conserving biodiversity, and can be seen as the beginning of CNS (Beier *et al.* 2015). In 2010, two papers revived the idea of CNS as a climate adaptation strategy, which provides a coarse-filter alternative identifying areas of expected high climate resilience without complex modelling or species-specific responses (Anderson & Ferree 2010; Beier & Brost 2010). Today, for example, Aichi Biodiversity Targets number five (reduce the rate of habitat loss) and 11 (ensure sufficient ecological representation among protected lands and waters) are both opportunities to integrate geodiversity into biodiversity conservation (CBD 2011; Comer *et al.* 2015).

One key motivation to use CNS is that data on abiotic physical variables are widely available and are more consistently mapped than data on vegetation communities or species distributions (Beier *et al.* 2015). Thus, CNS can also be adapted to conserve species in today´s climate in areas lacking data on where species occur (Beier *et al.* 2015), either independently, together with other environmental data or to complement species-level information. In areas without sufficient species occurrence data, a combination of specific environmental factors could be used to estimate biodiversity in a time-saving and cost-efficient way (Seijmonsbergen *et al.* 2018). Furthermore, adding geodiversity targets to a conservation plan which is designed to represent vegetation types and species usually does not increase the total area prioritized for conservation (Anderson *et al.* 2015).

1.3.2 Geodiversity elements and biodiversity

Different geodiversity elements or geofeatures (geological, hydrological and geomorphological) form the basis for biological diversity because organisms depend on abiotic components of ecosystems. For instance, geodiversity elements influence microclimates, control hydrology, create niche space and facilitate nutrient cycling (Nichols *et al.* 1998; Matthews 2014; Lawler *et al.* 2015). Higher geodiversity enables more niches within the same landscape, allowing a higher degree of biodiversity to co-exist (Parks & Mulligan 2010; Matthews 2014). Geology (e.g. rock types) and geological processes (e.g. weathering) contribute to the availability of important resources by providing nutrients and a substrate for vascular plants (Moser *et al.* 2005). The direct or indirect, mainly positive effect of soil heterogeneity on biodiversity has been found, e.g. in the case of vascular plants, mammals, reptiles and amphibians (Watling 2005; Walker *et al.* 2006; Ibáñez *et al.* 2012). Moisture availability is a crucial factor for the diversity of many species, which promotes the positive relationship between hydrological feature diversity and biodiversity (Gosselink & Turner 1978). Furthermore, different hydrological feature types have varying characteristics that create unique biodiversity patterns (e.g. floods in river environments vs. seasonal outbreaks and moisture variability in small streams) (Hjort *et al.* 2012).

In previous studies, a positive relationship between landscape-scale geomorphological heterogeneity and vascular plant species richness has been found (Nichols *et al.* 1998; Hjort *et al.* 2012). Physical disturbance at different landforms actively modifies the landscape and may either promote (at intermediate levels) or reduce (at stable levels or at environments of high disturbance rate) biological diversity (Huston 1994). Landforms differ e.g. in their soil moisture level, soil quality, ground-level lightness, proximity of ground water and variation of topography, which are all factors that affect species diversity patterns (Chipman & Johnson 2002; Lite *et al.* 2005; Hart & Chen 2006; Moeslund *et al.* 2013; Shroder 2013). The availability of soil moisture and the variability in soil moisture conditions associated with different landforms is a key factor affecting diversity patterns. For instance, species richness is usually greater on landforms where groundwater is close to the soil surface (Jansson *et al.* 2007; Ibáñez *et al.* 2012; Shroder, 2013). In mire areas, the proximity of groundwater leads to more minerotrophic conditions and thus to greater species richness (Lindholm & Hekkila 2006). Riparian zones are rich in biodiversity because there is moisture present and because they are ecotones between terrestrial and aquatic environments (Kalliola & Puhakka 1988; Malanson 1993).

Landforms that consist mostly of sand, such as beach ridges and dunes, can have varying growing conditions. If the sand is coarse, it filters water and nutrients away and makes the growing conditions poor (Aartolahti 1973). Dunes located in inland areas have typically a low pH-value, low amount of nutrients and low moisture content, which makes them low in biodiversity (Ujházy *et al.* 2011). However, high dunes are commonly more diverse than low dunes because of their varying topography which creates different growing conditions (Tilk *et al.* 2011). In general, the amount of nutrients and moisture tends to accumulate in the lower parts of the slopes of landforms, such as dunes, or to the bottom of pit-shaped landforms, such as gullies or kettle holes (Chipman & Johnson 2002; Lin *et al.* 2005). Additionally, species richness can vary within the slope orientation: e.g. dune or kettle-hole slopes that are facing north are usually more moist and thus more species rich than south-facing slopes (Aartolahti 1973; Ujházy *et al.* 2011).

2 Study aims

The primary goal of this study is to investigate how landforms and landscape-scale geodiversity (i.e. geological, geomorphological and hydrological feature richness) are related to biodiversity (i.e. the species diversity and rarity of vascular plants and other taxa). More specifically, I am seeking answers to five main research questions:

Q1. Is there an overall positive relationship between geodiversity and biodiversity in high-latitude environments? **(I, II, III)**
Q2. How do specific geodiversity measures (soil type, rock type, geomorphological and hydrological feature richness) account for threatened species richness of different taxa? **(I)**
Q3. How are geodiversity and vascular plant species richness related to each other across a gradient of human impact on the landscape (in environments of low, moderate and high human impact)? **(II)**
Q4. What kind of a relationship do landforms and plant diversity have in the boreal vegetation zone? **(III)**
Q5. Do the results of this thesis support the Conserving Nature´s Stage framework? **(I, II, III)**

There are seven hypotheses that are related to these study questions (Table 1). The research questions are answered and the hypothesis tested by the three research articles (papers) that this dissertation is based on. The research articles have varying contributions to the research questions and related hypotheses. The main contribution of each article (I, II and III) to separate research questions is marked in brackets after each question.

The papers included in this dissertation cover three different study settings. In paper I, the importance of geodiversity, topographical and climatic variables for multi-taxon threatened species richness and rarity was analysed in Finnish national parks at a 1-km^2 scale. In paper II, geodiversity and vascular plant species richness were examined at different land-use intensity (hemeroby) levels at the scale of 1-km^2 grid cells reaching through Finland. In paper III, the relationship between landforms and plot-scale vascular plant richness, diversity and rarity metrics at three spatial levels (alpha, beta and gamma) was evaluated at the Rokua UNESCO Global Geopark area.

Table 1. Hypotheses and their relationship with papers included in this study (I–III). The number in the name of the hypothesis indicates the study question to which it relates (e.g. H1 is related to study question Q1).

Hypothesis	**Paper I**	**Paper II**	**Paper III**
H1 (a) Geodiversity has an overall positive relationship with biodiversity (species richness, diversity and rarity).	X	X	X
(b) Geodiversity variables used in the analysis correlate positively (linearly or non-linearly) with species richness measures.	X	X	
(c) The inclusion of geodiversity variables in species richness models adds explanatory power and gives additional value to the models.	X	X	
H2 Rock-type richness, soil-type richness, geomorphological richness and hydrological richness are all important for threatened species richness, but there are differences in how they are correlated between threatened species from different taxa.	X		
H3 Geodiversity accounts for vascular plant species richness especially in areas where human impact is low.		X	
H4 Most of the landforms support higher vascular plant diversity than control sites, although the diversity patterns vary among landforms.			X
H5 It is expected that the results promote the use of CNS in conservation planning and management.	X	X	X

3 Study areas

The studies were conducted across Finland covering the boreal vegetation zones (Figure 2), and arctic environments in the northernmost parts. Two papers (I, II) covered spatially extensive areas. In paper I, there were 31 national parks included in the study (total area 8091 km^2), extending from southern Finland's coastal archipelago to northern Finland's glacially rounded hills with arctic-alpine conditions (Figure 2). The study was based on a regular grid of 1-km^2 grid cells, of which 6571 were included in the study. Finnish national parks follow the definitions and management objectives of IUCN and natural resources protected area management category II (Heinonen 2013).

In paper II, the study area consisted of 6191 1-km^2 grid cells dispersed across Finland (approximately 60°–70° N and 20°–31° E) (Figure 2). The landscapes of Finland 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 Finland is covered with weakly and moderately human-impacted land, with only under ten per cent of strongly human-impacted areas, located mainly around cities and municipality centres (Figure 2). Biogeographically, the study areas (I, II) cover hemi-, southern-, middle-, and northern-boreal vegetation zones (Ahti *et al.* 1968) and include a great variety of land cover types, such as forests, fell areas (alpine tundra), meadows and wetlands. The distribution limits of numerous plant species are met in the northern parts of Fennoscandia where the forests change into treeless tundra (Tikkanen 2005).

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 soils of Finland originated mainly during or after the last glacial period. The features that dominate 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 glacigenic (e.g. drumlins) forms, are common across the country (Atlas of Finland 1986). Glacially drifted till is the most common deposit (Seppälä 2005). Lakes and mires are common due to climate and recent deglaciation (Hyvärinen & Kajander 2005; Pajunen 2005).

The climate of Finland is fairly cold, but there are major differences between the southern and northern parts of the country. According to the Köppen-Geiger climate classification, the climate of Finland is classified as cold with no dry seasons (Df) (Kottek *et al.* 2006). Mean annual air temperature varied between −3 °C in the north to approximately 6 °C in the south between 1981– 2010, and the length of the thermal growing season (>5 °C daily mean temperatures) was from >185 days in the south to <105 days in the north. Mean annual precipitation was moderate through all seasons and ranged from 450 to 700 mm (Pirinen *et al.* 2012).

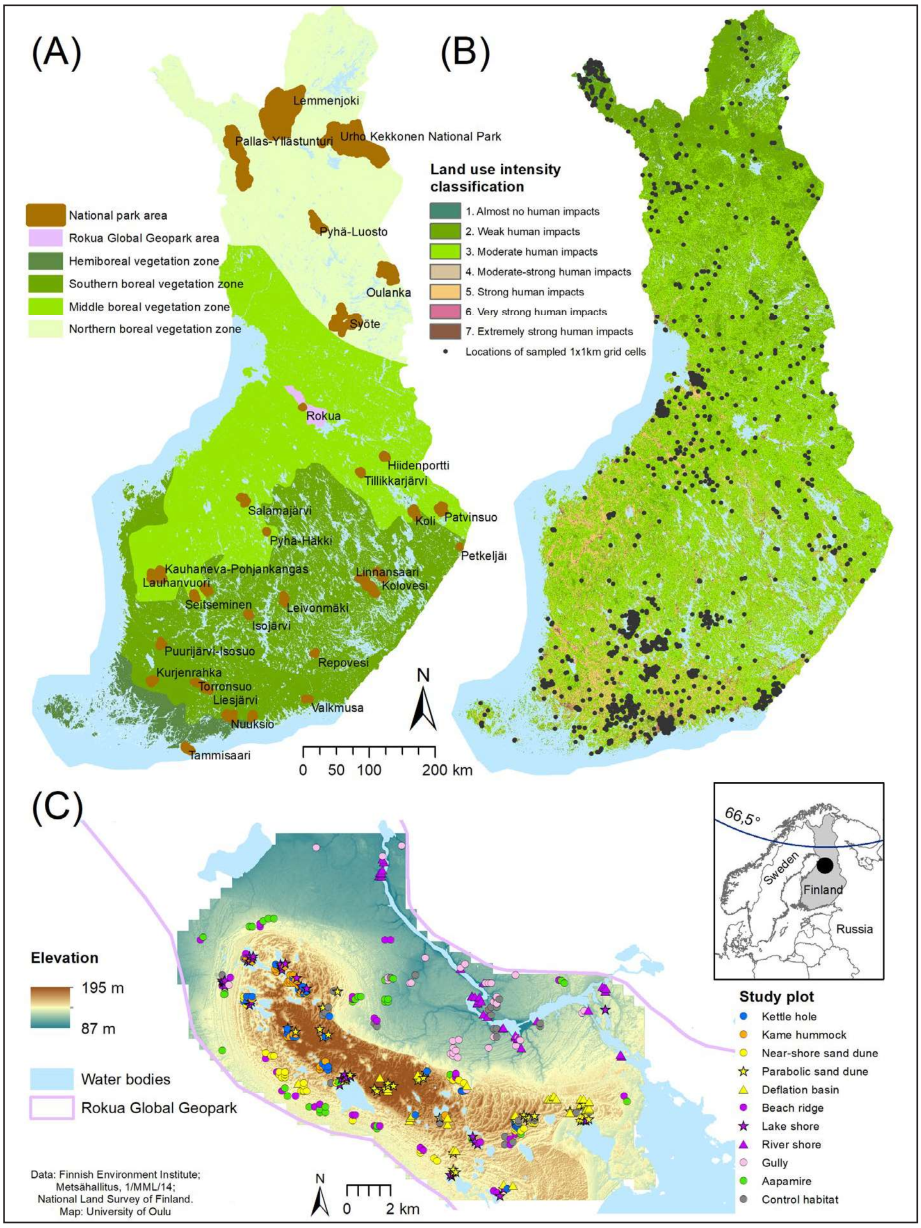

Figure 2. The location of the studied national parks and Rokua UNESCO Global Geopark together with major vegetation zones (A), land use of Finland and the location of sampled 1x1-km grid cells (467 in each of the three combined land-use categories) (B), and the locations of studied 1-m^2 vegetation plots on landforms and control habitat (n=385) at the study area in Rokua UNESCO Global Geopark (C). Land cover classification is based on a hemeroby index (Walz & Stein 2014) which was computed using CORINE Land Cover 2006, tree stand age (Luke 2011) and protected area data (Finnish Environment Institute 2013a). Note that national parks have been extended with thick borderlines to make them better visible on the map.

3.1 Rokua UNESCO Global Geopark

In paper III, the study area was within Rokua UNESCO Global Geopark in Finland (N64°34'43", E026°30'06") (Figure 2). It is Finland´s first and world´s northernmost Geopark, and was accepted to the network in 2010. The area is characterized by unique geology starting from 2.6 billion years ago and the landforms shaped by the last Ice Age, such as glacial ridges, extensive dunes and small ponds (kettle-hole lakes) filled with crystal-clear water (Figure 3). The 1326 km^2 Geopark area is comprised of three different landscape zones: the Rokua esker and dune area (Rokuanvaara area) (Figure 3), River Oulujoki Valley and Lake Oulujärvi.

Rokua UNESCO Global Geopark is located in the middle boreal vegetation zone with characteristics from both southern and northern boreal zones. Coniferous trees including Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate as tree species. Small shrubs, such as lingonberry (*Vaccinium vitis-idaeae*) and Labrador tea (*Rhododendron tomentosum*), dominate the field layer. The bedrock of the study area is mostly igneous migmatite granite gneiss, granite and schists (Aartolahti 1973; Huttunen *et al.* 2013). The soil is mostly composed of glaciofluvial deposits such a fine- or coarse-grained sand or silt. Additionally, moraine emerges where water erosion has removed the glaciofluvial deposits (Aartolahti 1973; Kløve *et al.* 2012; Ala-aho *et al.* 2015).

Geomorphology of the study area is dominated by an esker that lies across the study area in the southeast-northwest orientation. The area has a high rolling relief; the lowest parts are located in the Oulujoki River Valley (less than 90 metres above sea level) whereas the highest peaks are in Rokuanvaara hill area that reaches to almost 200 metres above sea level.

Rokua´s esker formed from sand transported and deposited by the continental glacier and meltwater around 12,000 – 10,000 years ago. Later on, it emerged as the result of land uplift (Aartolahti, 1973; Ala-Aho *et al.* 2015). Waves and wind moulded the sandy soil into beach ridges and near-shore and parabolic sand dunes. There is a gradual transition from the straight beach ridges to rolling dunes to parabolic dunes on the slopes of the esker formation (Huttunen *et al.* 2013). Parabolic dune fields are especially prevalent in the area. Separate dunes can have a length of over two kilometres with crests rising 25 metres above the surrounding terrain (Aartolahti 1973; Huttunen *et al.* 2013). Beach ridges are common in the plains that surround the Rokuanvaara hill area and in the esker ridge that heads west from the esker formation. Beach ridges are narrow and low but can have a length of even 10 kilometres and are usually covered with dry coniferous forest (Jalas 1953; Aartolahti 1973). There are deflation basins of different sizes between both beach ridges and dunes (Aartolahti 1973).

Peatlands (aapa mires) of the study area began to form in wet depressions after the glacial retreat (Pajunen 1995). Today, there are mires in kettle holes, several-kilometre-long narrow mire strips between beach ridges in the area surrounding the esker and also more extensive aapa mires patterned by strings, flarks and puddles (Huttunen *et al.* 2013).

Figure 3. Rokuanvaara area is one of the core areas of Rokua UNESCO Global Geopark. It is characterized by crystal-clear kettle hole lakes, such as lake Salminen (a), landforms shaped by the last Ice Age, such as large kettle holes like Syvyydenkaivo (b), and sunny and dry, lichen-covered south-facing slopes (c) that host, e.g. several insect species that are specialized in these dry environments. One of the typical vascular plant species growing in the lichen-covered sites is *Thymus serpyllum* subs. *serpyllum* (d), which is a regionally threatened species. Photos: Helena Tukiainen.

Kettle holes are common in the study area, and the largest of them are 1.5 km in diameter and 50 metres deep (Figure 3). They can have either dry, moist or pond-filled bottoms (Aartolahti 1973). Kame-hummocks are found in the north-west parts of the study area. They are approximately 100–150 metres in diameter and from a few to 30 metres above the surrounding terrain (Aartolahti 1973).

The lake and river system of the study area consist mainly of the River Oulujoki and lakes or ponds of various sizes. The River Oulujoki flows from Lake Oulujärvi to the Gulf of Bothnia, Baltic Sea. The age of the river is approximately 9,000 years in the study area, while in the lower course near the sea it is still elongating owing to land uplift. The streams flowing into the River Oulujoki have eroded steep-sided channels and gullies (ravines) on the sandy flats (Huttunen *et al.* 2013). Gullies have also formed on steep hills of kettle holes and kame-hummocks found in the Rokuanvaara area (Aartolahti 1973). Lake Oulujärvi is the fourth largest lake in Finland with a surface area of almost 900 m^2 and it borders the study area in the east. Kettle-hole lakes are more typical for the esker formation. They emerged when ice blocks buried in the sand melted, leaving large depressions in the terrain.

4 Material and methods

4.1 Biodiversity variables

Several measures of biodiversity were used to describe the biological richness of the study areas (Figure 4; Table 2). In paper I, threatened species richness from the following taxonomic groups were considered: vascular plants, fungi, lichens, bryophytes, beetles, butterflies and moths, molluscs, mammals, 2-winged flies, true bugs, birds, hymenopterans, caddisflies, stoneflies, amphibians, and spiders. Threatened species were those considered critically endangered, endangered, vulnerable, or near-threatened in Finland according to the IUCN Red List, with few exceptions (Rassi *et al.* 2001). Geographic coordinates of the records of threatened species were derived from the Hertta database (Finnish Environment Institute 2017).

In paper II, the total number of vascular plant species recorded in a 1-km^2 grid cell was used as a biodiversity measure. The vascular plant data 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 consensuses from 1985–2011. A total of 2108 vascular plant taxa were recorded and used in this study.

In paper III, several measures of biodiversity on different spatial levels (alpha, beta and gamma) were used to determine the diversity of vascular plants. Terrestrial vascular plant species abundance data (a total of 1535 1-m^2 quadrats) were collected during the field inventories in summer 2012 at the Rokua UNESCO Global Geopark area. From this data, alpha diversity was calculated using the mean vascular plant species richness, inverse Simpson diversity index and Shannon´s diversity index for each landform and each study plot (Tuomisto 2010). Gamma diversity was quantified as the number of vascular plant species recorded for each landform in total, and with Shannon`s and inverse Simpson indices.

Beta diversity was calculated using the contribution of single sites to overall beta diversity on studied plots (patterns in local contribution to beta diversity, LCBD), to identify ecologically unique landforms in relation to other landforms in the studied data (Legendre & De Cáceres 2013; Heino & Grönroos 2017) (paper III). LCBD mirrors the relative contribution of individual sampling units to beta diversity, and high LCBD value of a site suggests that the site includes an exclusive community composition across the whole data set. To calculate the LCBD values for each study plot, Hellinger-transformed abundance data and the function beta.div was used in R (R Development Core Team 2008; Legendre & De Cáceres 2013). In addition, beta diversity was calculated with the Biodiversity Assessments Tools package (Cardoso *et al.* 2015) beta.multi function which can be used to assess total beta diversity, that can be further separated into species richness and species replacement components.

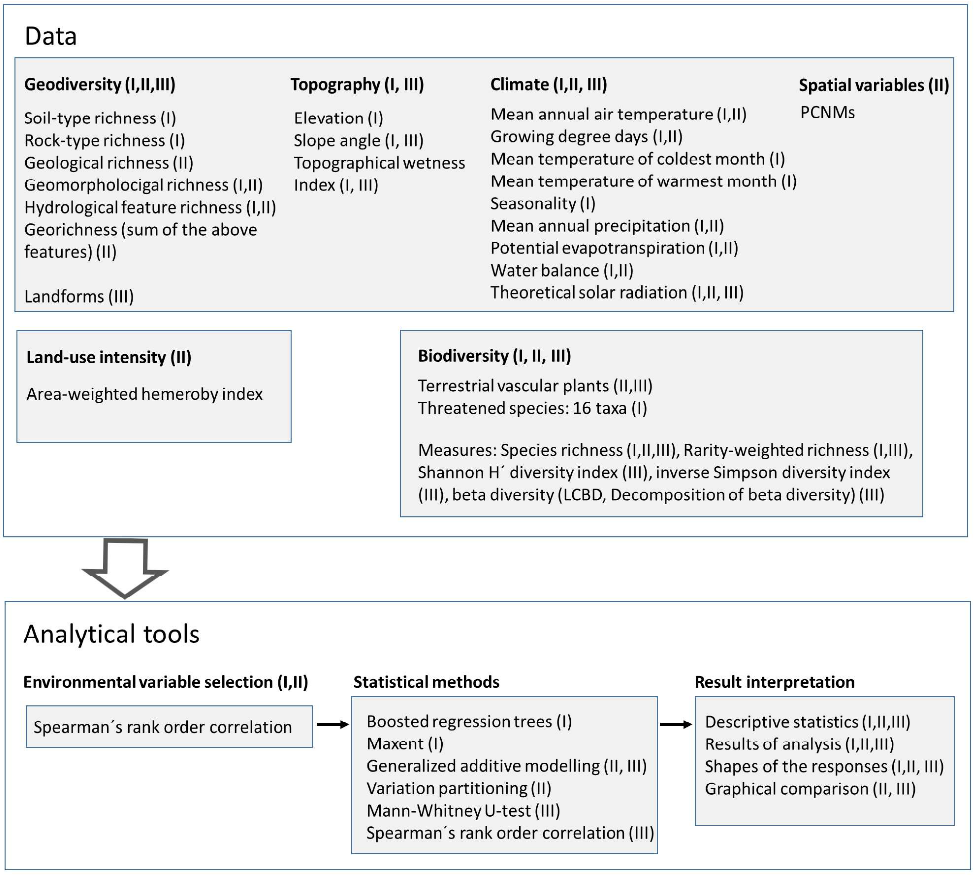

Figure 4. A schematic summary of the study steps including the used data and analytical tools. Threatened species were considered from the following 16 taxa: vascular plants, fungi, lichens, bryophytes, beetles, butterflies and moths, molluscs, mammals, 2-winged flies, true bugs, birds, hymenopterans, caddisflies, stoneflies, amphibians, and spiders. PCNMs is an abbreviation for the Principal Coordinates of Neighbour Matrices and LCBD for Local Contribution for Beta Diversity.

Table 2. The process of comparing geodiversity with biodiversity in this thesis defined by different stages and related questions (modified to the framework of this study from Seijmonsbergen *et al.* 2018). The contribution of each paper is in brackets after the related answer.

Stage	Question	The answer in this thesis
1	Which geodiversity values are to be captured, and for what purpose?	Functional values for both physical and ecological processes; to evaluate the relationship between bio- and geodiversity
2	Which geodiversity data are available?	Data on soil, rock, hydrology (I, II); modelled geomorphological data (I,II); data on landform locations (III)
3	What is the scale of the study/area?	Landscape scale with 1-km^2 resolution (I,II); local scale (III)
4	How is geodiversity evaluated and mapped (i.e. how is geodiversity quantified)?	By summing up the number of different geodiversity features (geological, hydrological, geomorphological) in a grid cell (I,II); by quantifying landforms (e.g. beach ridge, parabolic sand dune, kettle hole) (III)
5	What other data (in addition to geodiversity data) are needed?	Environmental data on topography (I, III), climate (I,II, III) and spatiality (II); land-use data (II); biodiversity data (I,II,III)
6	What analyses are needed?	Statistical modelling on the relationship between different variables (I, II, III); calculation of different levels and indices of biodiversity (I, III)
7	How can the results be utilized? Is there a specific product, such as a geodiversity map of an area, that can be utilized?	For instance: In conservation and land-use planning (I, II, III); in further scientific studies (I, II,III); in threatened species conservation (I); analysis results and graphics are the products of this study; other products, such as geodiversity maps can be produced from the data (I, II, II)

In addition to species richness measures, RWR was calculated in papers I and III (Figure 4). The rarity value of each species is the inverse of the number of grid cells in which it occurs. The RWR value per grid cell is the sum of the rarity values from each species recorded. Grid cells containing rarer species therefore have higher RWR (Williams *et al.* 1996; Albuquerque & Beier 2015).

4.2 Geodiversity variables

Measures of geomorphological, hydrological and geological richness were compiled following Hjort and Luoto (Hjort & Luoto 2010, 2012) in papers I and II. 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 modelled geomorphological features (landforms) in each grid cell. Hydrological richness was measured by summing the number of different hydrological feature types in a 1-km^2 grid cell, regardless of the number and cover of the specific features in the study grid cells. In paper I, hydrological features were mapped from the National Land Survey of Finland's database (NLS, 2007). Included hydrological features were: lakes (>1 ha), ponds (<1 ha), large rivers (>5 m wide), small rivers (2–5 m wide), streams (<2m wide) and springs. In paper II, the following features were considered as hydrological feature types: aquifers (Finnish Environment Institute 2013b), wetlands (NLS 2012), rivers, lakes and sea-areas (Finnish Environment Institute 2015).

Geological richness was measured by summing the number of different soil and rock types in a grid cell (paper II). In paper I, soil and rock-type richness were used as separate variables. 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 separate measures of geodiversity, a measure of total geodiversity (i.e. georichness) was computed in paper II by summing geological, geomorphological and hydrological richness values (following Hjort *et al.* 2012).

In paper III, the focus was on landforms. They were identified using field collected and remotely sensed data, existing maps and information from prior studies (e.g. Jalas 1953; Aartolahti 1973; Kløve Ala-aho, Okkonen, & Rossi 2012). Remote sensing data included aerial images (NLS 2010a) and LiDAR data-based digital elevation models (NLS 2008–2018). Map data included base maps (NLS 2010b) and soil data (GSF 2015). Ten distinct landform types, formed by different earth surface processes, were identified from the area: kettle holes (glacigenic), kame-hummocks (glaciofluvial), near-shore sand dunes, parabolic sand dunes and deflation basins (aeolian), beach ridges, lake shores and river shores (littoral), gullies (fluvial) and aapa mires (biogenic) (Figure 2). In addition, control sites which were not located on any distinct landform were used to test the null hypothesis. To make the data comparable, the sample size for each landform and control sites was set to 35 (n=35, kettle holes and river shores). In the case of other landforms that had more studied plots (37–110), 35 plots were randomly sampled.

4.3 Environmental variables

Climate data for 1981–2010 were derived from the Finnish Meteorological Institute at a 1-km^2 resolution (Pirinen *et al.* 2012) and digital elevation models (to calculate theoretical solar radiation; NLS, 2000) (papers I, II). Climate variables compiled for the study were mean annual air temperature (°C), mean temperature of the coldest month (January) (°C), mean temperature of the warmest month (July) (°C), seasonality (mean temperature of July–January) (°C), annual temperature sum above 5°C (i.e. growing degree days, GDD), mean annual precipitation (mm), potential evapotranspiration (mm year^{-1}), water balance (mm year^{-1}) and theoretical solar radiation (Mj cm^{-2} year^{-1}) (Figure 4).

Topographical variables that were used in paper I were derived from a 25-m-resolution DEM (NLS 2000). ArcMap 10.2 was used to calculate mean, standard deviation and range for elevation (m) and slope angle (degrees) per 1-km^2 grid cell. Topography-derived moisture conditions were calculated using the topographical wetness index (TWI) (Beven & Kirkby 1979). In paper III, topographic and climatic variables (slope angle, TWI and theoretical solar radiation) were derived from a Light Detection and Ranging (LiDAR) data based DEM (2 m cell size; NLS 2008-2018) that was resampled to 10 m resolution to match with the location accuracy of GPS located vegetation plots.

An analysis of Principal Coordinates of Neighbour Matrices (PCNMs) (Borcard & Legendre 2002) was employed to create spatial variables in paper II. PCNMs were constructed using the PCNM package in the R environment (Legendre *et al.* 2013). PCNMs are calculated from geographical distances between sites, and model spatial relationships among sites in decreasing order of spatial scale. 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.

4.3.1 Land-use intensity classification

Land-use intensity classification, which was used in paper II, is based on the concept of hemeroby (degree of naturalness), first introduced by the botanist Jaakko Jalas (1955). It measures the degree of human intervention on land-use, or the distance between the current vegetation and the potential natural vegetation of the site with no human intervention (Paracchini & Capitani 2011; Walz & Stein 2014). In the study, land use was classified into seven hemeroby classes: 1. ahemerobic (almost no human impacts), 2. oligohemerobic (weak human impacts), 3. mesohemerobic (moderate human impacts), 4. b-euhemerobic (moderate–strong human impacts), 5. a-euhemerobic (strong human impacts), 6. polyhemerobic (very strong human impacts), and 7. metahemerobic (extremely strong human impacts) (Figure 2). 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 addition, information on tree stand age (Luke 2011) and protected area status (Finnish Environment Institute 2013a) was utilized in making the classification.

After creating a grid of hemeroby that covered all of Finland, we calculated a simple area-weighted hemeroby index for 1-km^2 grid cells following Walz and Stein (2014):

$$\mathrm{M} = \sum_{h=1}^{n} f_n * h \qquad (1)$$

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. For use in further analysis, a classification with three categories of land-use intensity was created, 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, to maintain comparability among the data (Figure 2).

4.4 Statistical methods

Prior to analysis, the multicollinearity of geodiversity, climate and topography variables was examined in order to minimize collinearity problems (I, II) (Figure 4). This was done by using the Spearman´s rank order correlation (r_s) test. Selection of the final variables that were included in analysis was based on their mutual correlations, to their theoretical relevance (I, II) and their correlation with species richness (II). The limit of high correlation was $|r_s|$<0.7 in paper I and $|r_s|$<0.75 in paper II (Dormann *et al.* 2013; Aalto & Luoto 2014). In article I, the same number of geodiversity and other environmental (climate and topography) variables were chosen. Two climate (representing energy and moisture availability) (Hawkins *et al.* 2003) and two topographical variables were selected to match the four geodiversity variables. Thus, in paper I, rock-type richness, soil-type richness, geomorphological diversity, hydrological feature diversity, GDD, mean annual precipitation, elevation range, and the range of TWI were used in the analysis. In paper II, GDD, water balance and standard deviation of theoretical solar radiation were chosen for further analysis.

A pre-selection of spatial variables created by PCNMs was made in paper II. Since the aim was to account for spatial autocorrelation and influences other than those measured by geodiversity and climate variables, I retained spatial variables that both (i) showed short-distance spatial autocorrelation, and (ii) correlated as little as possible with the measured geodiversity and climate variables. Thus, only the spatial variables that were non-significantly (r_s p > 0.01) related to the selected geodiversity and climate variables were chosen.

Boosted regression trees (BRTs) were used to analyse the patterns of threatened species richness and RWR in paper I (Figure 4). BRT is an ensemble modelling method in which regression trees are applied and then boosted to combine a collection of models (Elith *et al.* 2008). The BRT models were fitted in the R statistical environment (R Development Core Team 2008) with the gbm package (version 2.1.1) (Ridgeway 2015) and the function gbm.step (Hastie *et al.* 2001). Models were interpreted based on predictors´ relative influence (RI) values, which can be thought of as model contributions. The analyses were done both for full datasets and datasets where the number of absences were reduced. There, only the 1-km^2 cells with threatened species records (presences) and absence cells immediately surrounding those presences were sampled. This was done to focus the resulting models on distinguishing cells that contained threatened species from otherwise similar cells that did not (on the basis that neighbouring cells tend to be similar because the environment is spatially autocorrelated). In this way, the amount of absence cells was reduced from 6317–6560 to 34–339 absences, depending on the taxonomic group.

The BRT models were run for the full set of threatened species from all taxonomic groups and separately for the threatened species richness of each of the taxa with a sufficient number of recorded threatened species to model individually (vascular plants, fungi, beetles, bryophytes, lichens, butterflies and moths, molluscs and mammals). With RWR as the response, the values only involved the grid cells with threatened species records, which decreased the data quantity and only vascular plants, bryophytes, fungi and all species combined were possible to model. Self-statistics were used to address internal model fit. Additionally, models were evaluated with 10-fold cross-validation (Ridgeway, 2015). To test whether model fit reflected more than spatial autocorrelation of the variables, the fits of all the BRT models were reassessed by separating geographically calibration and evaluation data (into eastern and western national parks) and calculating the root mean-squared error of predicted and actual values for the evaluation data.

In addition to BRTs, maximum entropy modelling (MaxEnt) was used in paper I to analyse taxon distributions (Appendix S3 in paper I). MaxEnt is a machine learning-based method, which has been used extensively in ecological studies to model species' distributions in relation to the physical environment, and is considered to work well with presence-only data and small sample sizes (Phillips *et al.* 2006; Elith *et al.* 2011). As in BRTs, MaxEnt models were performed with full and sampled data (which were further split into evaluation and calibration datasets) and were run separately for each taxonomic group with sufficient data quantity. The performance of each model was evaluated by using the area under the receiver operating characteristic curve and the importance of each predictor variable in each model was assessed using its relative contribution.

In paper II, the relationship between land-use intensity and both landscape-scale biodiversity and geodiversity was analysed with generalized additive modelling (GAM). More precisely, GAM-based response curves were used to graphically determine the diversity-hemeroby relationship. GAMs are particularly useful for creating 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 Trishibani 1990). Models were performed using the mgcv package of R (R Development Core Team, 2008). Both univariate (hemeroby index as the only predictor variable) and multivariate (climate variables and hemeroby index as predictor variables) model-based response curves were computed. GAM was also used in paper III (Appendix S2 in paper III) to explore the relationship between DEM-based variables (slope angle, TWI and theoretical solar radiation) and biodiversity variables (species richness, diversity indices, rarity-weighted richness and LCBD).

The contributions of geodiversity, climate and spatial variables in explaining vascular plant species richness in landscapes of low, moderate and high human impact were assessed using ordinary least-squares regression-based variation partitioning (VP) (Borcard *et al.* 1992; Anderson & Cribble 1998) (II). In models that were run in R, both linear and quadratic terms of the explanatory variables were used to capture the potential nonlinear responses, except for spatial variables. The models were optimized using a backwards elimination approach (criterion $p < 0.05$) and the performance of each model was evaluated by using adjusted R^2 (coefficient of determination). It provides unbiased estimation of the variation accounted for, and it is suitable in situations where the number of explanatory variables differs between the models, as in this case (Guisan & Zimmerman 2000).

In paper III, the difference between measures of alpha diversity (mean species richness, Shannon`s and inverse Simpson indices and RWR), LCBD and DEM-based variables was tested in the control habitat and distinct landforms with the non-parametric Mann-Whitney U-test for two independent samples (Ruxton 2006). It tests the likelihood that a randomly selected value from one sample will be less than or greater than a randomly selected value from a second sample (Mann & Whitney 1947). This was done only for the alpha diversity and LCBD values since they were the only ones that had unique values for each studied plot, contrary to measures of gamma diversity (and results from beta. multi calculations). A Bonferroni correction (p-value multiplied by the number of tests performed) is used to control potential Type 1 error, i.e. concluding that a statistically significant difference is present when it is not (Armstrong 2014). In addition, Spearman´s rank order correlation was calculated to examine the relationships between measures of plant species diversity, and the three DEM-based topographical variables.

5 Results and discussion

5.1 Summary of the results

The results of this thesis are a combination of results from the three papers (I–III). In *paper I*, the relationship between threatened species richness patterns and geodiversity measures in Finnish National parks with 1-km^2 resolution was examined. The data were analysed with BRTs to gain a better understanding of which climatic, topographical and geodiversity measures (soil-type richness, rock-type richness, hydrological richness and geomorphological richness) account for threatened species richness and RWR patterns from different taxa. The results showed that although the contribution of geodiversity was not pronounced for all taxonomic groups, it was significant in many cases (e.g. for vascular plants and bryophytes) and added consistent explanatory power to the models (Table 3; Figure 5; see also Table 3 and Table 4 in paper I). From the geodiversity variables, geomorphological richness was the most important for most taxa, although other variables had strong and consistent contributions, too (Table 3; Figure 5). The results from modelling the aggregate distribution of threatened species with MaxEnt were qualitatively similar to those for modelling threatened species richness with BRTs (see Appendix 3 in paper I for further details).

In *paper II*, the focus was on the variation of geodiversity and biodiversity (measured as vascular plant species richness) at different land-use intensity levels, and the factors affecting biodiversity in environments of low, moderate and high human impact. The study area consisted of 1-km^2 grid cells dispersed across the whole country of Finland (Figure 2). GAM-based response curves were used to graphically determine the diversity land-use intensity relationships and VP to examine the contribution of geodiversity, climate and spatial variable groups in explaining vascular plant richness in the three levels of human impact across the landscape. The results showed that the geodiversity land-use intensity relationship was generally negative, whereas biodiversity and land-use intensity had a positive relationship (see Figure 3 in paper II). Geodiversity was the most pronounced explanatory variable group for species richness in pristine environments (independently explained variation) (Table 3). If joint variations are taken into account, geodiversity best accounted for vascular plant species richness in areas of moderate and high human impact (see Figure 4 in paper II).

Paper III examined the relationship between ten different landforms (kettle hole, kame-hummock, near-shore sand dune, parabolic sand dune, deflation basin, beach ridge, lake shore, river shore, gully and aapa mire) and a control habitat (no landform present) to vascular plant species richness in the Rokua UNESCO Global Geopark area at a 1-m^2 plot scale. There, vascular plant species richness (average and total), Shannon´s diversity index and inverse Simpson diversity index were calculated as measures of alpha-level and gamma-level diversity. Furthermore, RWR was calculated as an additional measure for the

Table 3. A summary of the main results from the three papers included in this thesis.

Paper I	Paper II	Paper III
High geodiversity values were consistently associated with high threatened species richness across taxa.	Geodiversity correlated negatively and biodiversity positively with land-use intensity.	In general, landforms had higher plant diversity than control sites where no landforms existed.
Geomorphological richness was the most important geodiversity predictor for most taxa.	The highest independent geodiversity contribution for species richness was in pristine environments.	Different landforms had different levels of biodiversity, e.g. gullies were high and dunes generally low in their diversity.
Geodiversity measures correlated most strongly with species richness of threatened vascular plants and bryophytes.	If variation explained jointly with climate and spatial variables is considered, geodiversity best accounted for vascular plant species richness in areas of moderate and high human impact.	Alpha and gamma diversity had quite similar patterns, whereas beta diversity differed in the case of, e.g. aapa mires.

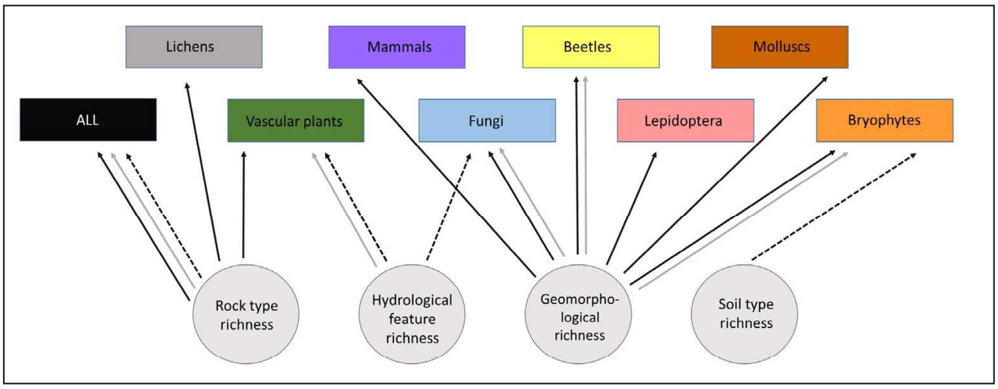

Figure 5. Geodiversity predictor with the highest relative influence value for threatened species richness in boosted regression tree models for different taxa. The relationship is illustrated with black arrows (threatened species richness as a response, full dataset), grey arrows (threatened species richness as a response, sampled dataset) and dashed arrows (rarity-weighted richness of threatened species as a response) (paper I). The all category includes species from 16 taxa (vascular plants, fungi, lichens, bryophytes, beetles, butterflies and moths, molluscs, mammals, 2-winged flies, true bugs, birds, hymenopterans, caddisflies, stoneflies, amphibians, and spiders). Due to data quantity, models could not be run for all taxa in sampled data and in RWR analysis (i.e. too few species per taxon).

alpha-level. Beta diversity was expressed with LCBD values and decomposed to richness-difference and replacement components (see Appendix S1 in paper III). According to the results, landforms were generally more diverse than control sites at each spatial level (Table 3 & 4). As an exception, dunes were less diverse than control sites in some cases. Landforms varied in their biodiversity: this was most pronounced in gullies and river shores, whereas dunes, kame-hummocks and beach ridges had mostly low or moderate diversity values. Alpha and gamma diversity had quite uniform patterns of diversity, and these patterns were also visible in the variation of beta diversity, with few exceptions (Table 4). The LiDAR DEM-derived variables (slope angle, TWI and theoretical solar radiation) did not succeed well in explaining the variation in the biodiversity measures (see Appendix S2 in paper III for further details).

5.2 Discussion based on the research questions

5.2.1 The overall relationship between geodiversity and biodiversity (Q1)

Through the results of this thesis, a consistent positive relationship between geodiversity and biodiversity measures was found (Table 3). This supports study hypothesis **H1a** where I proposed that geodiversity has an overall positive connection with biodiversity. High geodiversity values were also consistently associated with high species richness across taxa (I, II), supporting **H1b**. In more detail, all predictors, including geodiversity predictors, showed a positive relationship between the variable and predicted threatened species richness in the BRT models (I). On the contrary, the correlation between threatened species RWR and geodiversity variables was not always positive (**H1b** proposed a positive relationship between geodiversity and biodiversity measures), although the ones with a negative relationship had a reasonably small modelled relative influence on RWR. The results from paper II also support **H1b** since all the geodiversity variables that were selected to the VP models had either a positive linear (geological richness, hydrological richness) or quadratic (geomorphological richness) relationship with vascular plant species richness.

I found strong support for **H1c** where it was proposed that geodiversity variables are meaningful in species richness models. In paper I, geodiversity variables added significant explanatory power to BRT models, where the diversity of threatened species from altogether 16 taxa was analysed. The results indicate that geodiversity seems to be particularly useful for understanding patterns of threatened species' RWR, although climatic variables were the dominant predictors. In analysis of threatened vascular plant and fungal species' RWR, the combined contribution from geodiversity variables exceeded the equivalent contribution in species richness models. Additionally, the geodiversity variable group had both independent variation and shared variation, especially with climate, for vascular species richness in VP models in paper II (supporting **H1c**).

Table 4. Measures of vascular plant diversity (and their spatial level: alpha, beta or gamma) for each landform and control sites in the study area at Rokua UNESCO Global Geopark (paper III). The largest value of each measure is bolded and the smallest value is underlined. LCBD is for Local Contribution for Beta Diversity and RWR is for Rarity-Weighted Richness.

Process	Landform	Species richness		Shannon H’		Inverse Simpson		LCBD	RWR
		α	γ	α	γ	α	γ	β	α
Glacigenic	Kettle hole	4.69	33	0.89	2.68	2.27	10.49	0.0032	0.25
Glaciofluvial	Kame-hummock	2.66	18	0.64	1.58	1.79	3.78	0.0018	0.07
Aeolian	Near-shore sand dune	<u>2.26</u>	<u>7</u>	0.56	1.41	1.76	3.22	<u>0.0018</u>	<u>0.02</u>
	Parabolic sand dune	2.43	16	0.56	1.61	1.77	3.74	0.0021	0.06
	Deflation basin	3.71	20	0.90	1.95	2.58	5.36	0.0022	0.11
Littoral	Beach ridge	3.51	19	0.82	1.73	2.14	4.25	0.0018	0.05
	Lake shore	4.46	40	0.96	2.34	2.48	6.66	0.0030	0.36
	River shore	5.97	57	1.17	2.92	2.91	10.46	0.0035	**0.89**
Fluvial	Gully	**6.60**	**59**	**1.31**	**3.05**	**3.37**	**10.94**	0.0033	0.84
Biogenic	Aapa mire	5.69	24	1.14	2.45	2.65	9.13	**0.0038**	0.22
No process	No landform / Control site	2.51	15	<u>0.55</u>	<u>1.39</u>	<u>1.59</u>	<u>2.93</u>	0.0019	0.04

Although the additive effect of geodiversity on species richness models was meaningful, the contribution of geodiversity to biodiversity was not extensively high (I, II). Climatic variables, especially GDD, mostly dominated the models – although in VP models (II) there was a notable shared contribution between the two variable groups (i.e. climate and geodiversity). Thermal conditions and energy availability are among the major limiting factors of species patterns in high latitudes, especially at large geographic extents (Hawkins *et al.* 2003; Field *et al.* 2009; Niskanen *et al.* 2017; Suwal & Vetaas 2017). In paper I, GDD and mean precipitation were usually the dominant predictors of threatened species richness and they had a positive relationship between biodiversity, which indicates that most of the threatened species favour relatively warm and wet areas. However, the importance of climate variables was less pronounced and the importance of geodiversity variables was more pronounced in the sampled data where the number of the absence grid cells was controlled. There, I had a dataset of cells that were climatically suitable for at least some threatened species. Thus, climatic gradients may determine the regional species pools, and geophysical factors and local environmental heterogeneity have a greater influence on biodiversity at finer scales (Field *et al.* 2009). Based on the results from paper I, it could be proposed that geodiversity variables represent the next set of abiotic requirements once the climatic-tolerance filter has been passed.

Past disturbances and other historical legacies and biotic interactions are notable factors that were not taken into account in this study, but have an effect on the biodiversity-environment relationships (Dornelas 2010; Wisz *et al.* 2013). It should also be considered that modest correlations between geodiversity and species richness may be a consequence of a nonequilibrium between present-day biotic communities (e.g. vegetation) and abiotic nature due to recent and ongoing climate change.

5.2.2 Geodiversity measures and threatened species richness (Q2)

In paper I, I found that specific geodiversity measures (i.e. rock-type richness, soil-type richness, hydrological feature type richness and geomorphological richness) had varying contributions to species richness and RWR of different taxonomic groups, thus giving support for hypothesis **H2**. In general, geodiversity measures correlated most strongly with the species richness of threatened vascular plants and bryophytes. Of the geodiversity variables, geomorphological richness was the most important for most taxa, whereas rock-type richness was the most important for lichens and vascular plants (Figure 5). In addition, rock-type richness was the most pronounced geodiversity predictor of all taxa combined. Geomorphological features (landforms) promote unique abiotic conditions, which promote species richness (Nichols *et al.* 1998; Hjort *et al.* 2015). Landforms differ, e.g. in their soil moisture conditions and in their microtopography, creating various microhabitats and niches that species with different traits can occupy (Huston 1994; Lite *et al.* 2005; Hart & Chen 2006). Variation in rock types creates variation in the substrate and has been firmly linked to vascular plant and lichen diversity elsewhere (Pausas *et al.* 2003; Spitale & Nascimbene 2012; Kougioumoutzis & Tiniakou 2014). As an example, the inclusion of nutrient-rich (calcareous) habitats supports the existence of several threatened vascular plant species in Oulanka National Park, such as *Gypsophila fastigiata*, a plant specialized in living on calcareous cliffs (Parviainen *et al.* 2008; Rassi *et al.* 2010).

In addition, soil and hydrology both contributed to the threatened species richness models: soil for RWR of bryophytes and hydrology for vascular plants and RWR for fungi (Figure 5). Soil diversity (or pedodiversity) has been recognized as an important driver of biodiversity (Ibáñez *et al.* 2012; Stein *et al.* 2014). The availability of moisture is one of the principal components determining plant growth (Svenning & Skov 2006). Many threatened species favour habitats near water (such as streams and ponds) (Rassi *et al.* 2010), even though aquatic environments are not the main habitat for many plant or fungal species in the studied data. Hydrological features vary in their local-scale environmental characteristics which affects their species compositions. For instance, streams create unique microhabitats and moisture conditions that a number of threatened species favour (Rassi *et al.* 2010), whereas in larger rivers floods may positively impact species diversity.

5.2.3 Geodiversity and species richness across a gradient of human impact (Q3)

Georichness, or the sum of geological, geomorphological and hydrological richness values, tended to be greatest in areas of low human impact (e.g. forests that are not under forest management) and lowest in areas of high human impact (such as urban areas) (paper II), supporting the hypothesis **H3** (Figure 6). This is consistent with suggestions from recent research, where a negative effect of human actions on geodiversity was noticed (Gordon & Barron 2013; Räsänen *et al.* 2016). However, there was a slight increase in georichness with land-use intensity in moderately impacted areas (such as natural grasslands, coniferous forests and pastures). Agriculture is common in extensive river valleys and forest management is common in topographically variable landscapes, which typically harbour relatively high geodiversity (Serrano *et al.* 2009; Hjort & Luoto 2010; Pellitero *et al.* 2011).

Inversely, a positive relationship between human impact on land-use and species richness of vascular plant species was found (II). Vascular plant species richness increased from the most pristine to moderately human-impacted areas, after which the relationship levelled off. Elsewhere, similar results have been attained and the proposed reasons for the rich biodiversity in human-impacted areas are multiple (e.g. invasive species dispersal, habitat heterogeneity in moderately urbanized areas, and more favourable climatic conditions for plants in urban areas in cold climate environments) (Kühn & Klotz 2006; McKinney 2008; von der Lippe & Kowarik 2008; Vilmi *et al.* 2017).

The independent contribution of geodiversity to vascular plant species richness in VP models was not high, but had a constant decreasing trend from low to highly human-

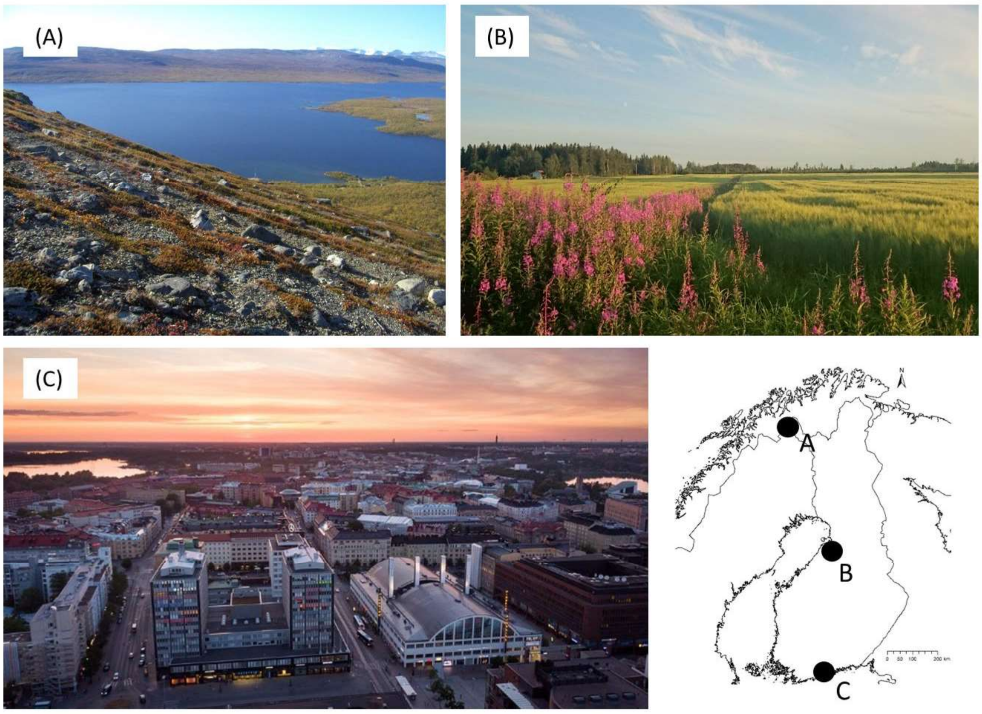

Figure 6. Example of locations where human impact on landscape is low (A; fell area in Kilpisjärvi), moderate (B; agricultural landscape in Kempele), and high (C; urban area in Kamppi, Helsinki), following the three-level land-use intensity category classification in paper II. Photos: Helena Tukiainen (A, B), Pixabay, CC0 licence (C).

impacted environments (II) (consistent with Hjort *et al.* 2012; Lawler *et al.* 2015). This gives support for **H3**, where it was proposed that geodiversity accounts for species richness especially in areas where human impact is not high. In contrast, if the shared contributions are taken into account, the importance of geodiversity was highest in environments of moderate human impact, and also notably high in highly human-impacted environments (only partly supporting **H3**). Especially the shared importance of climate and geodiversity variables was high, which may indicate that climate and terrestrial abiotic heterogeneity interact quite strongly in anthropogenic environments (Räsänen *et al.* 2016). While rural areas tend to be quite diverse in their geodiversity (as stated in the previous chapter), urban areas tend to be located near abiotic ecosystem services or water bodies, which increase abiotic diversity of human settlements (Figure 6).

5.2.4 The relationship between landforms and vascular plant diversity (Q4)

Geodiversity elements (or geofeatures, such as landforms) are most often assessed by their value for geoconservation, or for their scientific, educational or recreational use (Brilha 2018). This far, ecological values, or the ability of landforms to sustain biological diversity and ecosystems, are less frequently considered (Gordon *et al.* 2012; Gray 2013). In paper III, I observed landforms by their value for biodiversity at the Rokua UNESCO Global Geopark area. The results showed that different landforms had differences in terrestrial vascular plant diversity, and that they were generally more diverse than the control sites (which supports **H4** where I proposed that most of the landforms support higher biodiversity than the area that does not have landforms). This gives support for the use of biodiversity information in geofeature evaluations. For instance, if the overall geodiversity (or the variety of geofeatures) of an area could be complemented with the individual geoconservational and ecological values of landforms or geosites (see e.g. Pellitero *et al.* 2015), it could increase interest among management and conservation practitioners to include geodiversity in their practical work.

I found varying patterns among landforms and vascular plant diversity (III), as I proposed in **H4**. In contrast, DEM-based topographic variables did not succeed well in distinguishing biodiversity between landforms or as predictors of alpha and beta level biodiversity measures (see Appendix S2 in paper III). Gullies and river shores were most diverse at all spatial levels (alpha, gamma and beta). In addition, kettle holes, lake shores and aapa mires were quite rich in their alpha, gamma and beta diversity (Table 4). These landforms are generally moist environments that promote biological diversity. In addition, microhabitats and climates that create heterogeneous niche-space are important determinants of biodiversity (Lundholm 2009; Jones, Szyska, & Kessler 2011) and are also important for buffering species against climate change by providing local climatic options (Anderson *et al.* 2014). For instance, kettle holes can maintain varying types of environments, e.g. dry and sunny south facing slopes, shady and moist north-facing slopes and moist bottoms, which create different microhabitats and climates and thus promote vascular plant diversity (Aartolahti, 1973; Jones *et al.* 2011).

Near-shore dunes, parabolic dunes and kame-hummocks had low alpha and gamma diversity, together with control sites (Table 3). They are mainly composed of sand or gravel, which leads to low variability and availability of soil moisture. Parabolic dunes are well developed in the area and have more variation, e.g. in moisture and microclimatic conditions than near-shore dunes due to the increase in height (Tilk *et al.* 2011; Ujházy *et al.* 2011). In the results, parabolic dunes had slightly higher alpha and gamma diversity values than near-shore dunes, and the difference was more pronounced in LCBD values (Table 4). This reflects the importance of parabolic dunes to the total species composition in the area. In general, LCBD had slightly different patterns among landforms than alpha and gamma diversity measures. For instance, the ecological uniqueness of aapa mires was emphasized, as they were the landform that had the largest LCBD values. In addition, their total beta diversity was dominantly dependent on the species replacement component, meaning that differences in species composition is the main reason for the high total beta diversity value of aapa mires. These results highlight the importance of examining all the spatial scales of diversity to gain a holistic picture on the biodiversity of an area (Fleishman *et al.* 2006).

5.2.5 Do the results of this thesis support the Conserving Nature´s Stage framework? (Q5)

The CNS framework is based on the idea that most species depend on an abiotic "stage" on which they exist, and biodiversity is generally greater in areas where abiotic heterogeneity is high (Lundholm 2009; Anderson & Ferree 2010; Beier *et al.* 2015). According to the results from the three papers, geodiversity and landforms had a positive relationship with biodiversity. Although geodiversity measures were not the strongest correlates of biodiversity, they had consistent positive relationships and positive effect on species richness. On a local scale, sites with landforms had in most cases greater plant species diversity than sites that had no landforms. These results give support for the basic principles of CNS and to the utilization of the framework in conservation planning and management, as I hypothesized (**H5**).

In paper II, the role of geodiversity in human-altered landscapes was explored. There, geodiversity decreased in importance from small to negligible towards highly human-impacted land use, whereas species richness was highest in urban and agricultural areas. Thus, it is not yet clear whether CNS is a valid principle in human-impacted landscapes, which are becoming increasingly common. Only a quarter of land on Earth is substantively free of the impacts of human activities today, and this is projected to decline to just one-tenth by 2050 (WWF 2018). For future research, it is of high importance to examine the geodiversity-biodiversity relationships in environments where human impact on land use is moderate to high at different spatial scales and in different geographical locations.

In addition to CNS, also other conservation approaches and adaptation strategies, such as climate envelope models, assisted colonization and mobile reserves, have been developed to meet the challenges brought about by global change. For instance, there has been an attempt to chain together models and scenarios (emission scenarios, global air-ocean circulation, regional circulation and biotic response) to prioritize land for reserves in the changing climate (Beier & Brost 2010). Compared to these more complicated scenario-based approaches, CNS would probably fare well in practicality, cost, and because it does not depend on a particular future climate (Beier & Brost 2010; Beier *et al.* 2015).

5.3 Strengths and limitations of the geodiversity concept

A multiplicity of definitions have emerged for geodiversity and its subdivisions. The elements that it consists of have been called, e.g. geodiversity elements, geodiversity features, geoheritage elements, geodiversity sites, geosites (see the review by Brilha 2016), and geomorphosites (Seijmonsbergen *et al.* 2018), all with slightly different emphasis. Furthermore, geodiversity can also be referred to as, e.g. abiotic environmental heterogeneity (a broad definition), geological diversity or geomorphodiversity (which are components of geodiversity). There are also several qualitative and quantitative ways to measure geodiversity (Zwoliński *et al.* 2018). This multiplicity of concepts and ways of measuring geodiversity can lead to the use of the geodiversity-concept in unconventional ways, and it could be useful to propose a systematic approach for the use of the concept. However, in terms of studying the relationship between biodiversity and geodiversity, it is likely that rather than creating a uniform measure of geodiversity, the best measure to use will vary between study area and taxon. Notwithstanding, methods should be transparent and transferable when possible. However, including more specific information on the measures has the potential to furthermore improve the possibility to find the theoretically strong connection between bio- and geodiversity.

Based on papers I and III, it seems valuable to distinguish between explicit geodiversity measures of geology, landforms and hydrology, and more commonly used, purely DEM-based topographical data (e.g. Parks & Mulligan 2010). Topography and its variability is important for biodiversity: topographical variability provides a range of microclimates within an area, including microclimates that are decoupled from the regional climate (Dobrowski 2011; Comer *et al.* 2015). Regions with high topographical heterogeneity have steep climatic and habitat gradients in relatively small areas, which promotes spatial turnover of species favouring different conditions (Stein *et al.* 2014). Furthermore, different geodiversity features (e.g. hydrological features, rock types and landforms) support varying (micro)topographical conditions. In BRT models (I), topographical variables, especially elevational range (which is a widely used topographical metric) and TWI range were important especially for threatened vascular plants and bryophytes, respectively. Thus, geodiversity data (i.e. data on soil and rock types, geomorphology and hydrological features) could be used alongside other topographical and climatic data to better target areas that support rare or species-rich communities (Albuquerque & Beier 2015; Bailey *et al.* 2018). It is valuable to distinguish between these different aspects of abiotic environmental heterogeneity and to analyse the effects of explicit geodiversity measures for biodiversity. Based on this study, I stress the need for wider incorporation of geodiversity – not just DEM-based topographical variables – in scientific research and in both conservation theory and management.

The method of simply just summing up the different geofeatures in the study unit regardless of, e.g. their area or number, seemed to be efficient and provides a time-saving and financially practical way of measuring geodiversity (I, II) (Serrano *et al.* 2009; Pellitero *et al.* 2011; Hjort *et al.* 2012; de Paula Silva *et al.* 2015; Bailey *et al.* 2017). Although I got very encouraging results by using this simple way of measuring geodiversity, it should be considered that this type of calculation is dependent on the scale changes and the selection of geodiversity elements to be included (Erikstad 2013). In this thesis (I, II), the study units were constant 1-km^2 grid cells, to avoid problems related to varying-sized study units. It is especially important to keep the area constant in studies on environmental heterogeneity-diversity relationships, since the use of equal-area study units emerged as a key factor that influenced the relationship between environmental heterogeneity and species richness (Stein *et al.* 2014; but see Alahuhta *et al.* 2017). In article III, the landforms had a varying area, but the unit at which the vegetation was determined (1-m^2 vegetation quadrat) was constant for each plot. Since especially alpha and gamma diversity tend to arise when the number of sampling units increases, the number of landforms was controlled to be 35 at each landform type.

5.4 Management implications

In times of rapid environmental change, gaining holistic insights into biodiversity-environment relationships seems to be more topical than ever. Still, geodiversity and geoconservation are not accepted or properly recognized in most countries of the world and geodiversity is usually treated as a part of broader concepts such as ecological diversity in natural resource policy (Erikstad 2013; Comer *et al.* 2015). In recent years, there has been some positive development in implementing geodiversity into legislation and conservation strategies. For instance, the leading nature conservation organization, IUCN, which sets the guidelines for nature conservation, has accepted geodiversity conservation strategies as part of their interest (e.g. IUCN World Commission on Protected Areas Geoheritage Specialist Group). In addition, some countries, such as Spain, have included geodiversity conservation into their legislation. In many cases, geosites or extraordinary geophysical features have gained protective status (e.g. the UNESCO Global Geoparks network).

It is often a great challenge to introduce conservation, both geo- and biodiversity conservation, as a positive element in local management and development strategies (Erikstad 2013). Several questions arise when the implementation of geodiversity into conservation is addressed. How should geodiversity be implemented in conservation planning, especially if it is combined with biodiversity information? How should practical management be handled? At the scale of local management, the spatial extent of geodiversity and geofeatures might become a practical issue: How is it possible to manage them if they cross administrative borders, such as municipality borders?

The indication of spaces where natural diversity is concentrated could be very valuable for conservation area management purposes. If geodiversity data are complemented with biodiversity data from the same area, it is possible to obtain a holistic natural diversity assessment, that summarizes vegetation, fauna, climate, geology, hydrology and geomorphology (Serrano & Ruiz-Flaño 2007; Gray *et al.* 2013; Pellitero *et al.* 2015). It has been proposed that a protected area network of geodiverse areas could be designed in a way that the combinations of available areas would capture (1) the maximum diversity (hotspots of richness; select the areas that are rich in geodiversity), and (2) areas where rare geodiversity elements are situated (i.e. include areas where rare geodiversity features occur) (Williams *et al.* 1996; Ibáñez *et al.* 2012). Based on the results of this study, a third possibility could be to capture the areas where different types of geodiversity (hydrological, geological or geomorphological) and various landforms that support different aspects of biodiversity occur.

To meet all challenges in the future, it is necessary to strengthen the management between geodiversity and ecology, cultural heritage and landscapes. It is important to both acknowledge that geodiversity merits conservation for its own particular geoheritage values, but also examine the benefits of a more integrated approach where both biodiversity and geodiversity perspectives are included. Furthermore, the interests of different stakeholders, e.g. in the Finnish context the interests of indigenous or local people, mining industry, tourism and forestry representatives, often have an interest in the same area – which may be also valuable in its biodiversity and/or geodiversity values. A balance between the use and protection of such areas must be found. In the face of ongoing climate change and the targets for reducing biodiversity loss by 2020 (CBD 2011; Allen *et al.* 2018), conservational values should not be underestimated. In addition to local-scale conservation, also multinational approaches, such as co-operation in Arctic areas under the Arctic Council (Meltofte *et al.* 2013), are essential to meet the needs that environmental conservation has to meet under ongoing global change.

5.5 Themes for future research

The quantitative studies concerning geodiversity-biodiversity relationships have thus far focused on spatially limited areas, e.g. comprising the extent of one country or a few vegetation zones (e.g. Anderson & Ferree 2010; Hjort *et al.* 2012; Bailey *et al.* 2017, 2018). To gain a more comprehensive picture, it would be necessary to examine biodiversity-environment relationships at various geographical locations and at multiple scales. Local-scale analyses are needed to examine the detailed relationships that could provide essential information for management-scale purposes, such as conservation area design. In addition, landscape-scale and particularly global-scale analyses are essential in providing a holistic, spatially extensive framework of relationships. In the face of ongoing climate change and the CNS approach, it would be essential to gain information on temporal changes in biodiversity and how they relate to the geodiversity of an area (Bhatta *et al.* 2018; Maliniemi 2018). Additionally, there are just a few studies where aquatic biodiversity and geodiversity have been examined (e.g. Sutcliffe *et al.* 2015; Kärnä *et al.* 2018).

In addition to taxonomic diversity, biodiversity can also be characterized according to how species relate with each other, i.e. by measuring their phylogenetic or functional diversity (Cardoso *et al.* 2015; Teichert *et al.* 2018). It would be a novel approach to examine the linkage between geodiversity measures and these two other facets of biodiversity. Moreover, species traits and geodiversity information have not yet been examined together. The inclusion of these beyond-taxon measures of biodiversity in relation to geodiversity would provide new information on geodiversity-biodiversity relationships. Moreover, ecological weighting of landforms or geodiversity elements (e.g. based on their taxonomic or functional diversity) could considerably benefit conservation in theory and practice.

6 Concluding remarks

By analysing the relationship between geodiversity and biodiversity measured with multiple up-to-date approaches and modelling methods, this thesis has provided new perspectives on biodiversity-environment relationships across boreal and arctic landscapes. Subsequently, the results highlighted the importance of landforms, as well as landscape-scale or meso-scale georichness measures in determining species diversity patterns. Furthermore, this thesis provided strong evidence for the argument that Conserving Nature´s Stage is a valid conservation framework, at least in natural-state areas.

To conclude, the five main points of this thesis are summarized in the following section (according to the original study questions):

1. **Geodiversity had an overall positive relationship with biodiversity and added explanatory power for biodiversity models in several study areas, in the case of several taxa and for both threatened and common species.** Geodiversity variables had predictive power together with climate (especially energy-related climatic variables), which was the strongest predictor group of species richness in the models. The importance of geodiversity variables for threatened species richness was especially notable when the study setting was delineated within climatically suitable grid cells.
2. **Specific geodiversity measures (soil-type richness, rock-type richness, geomorphological richness and hydrological feature richness) accounted uniquely for threatened species patterns of different taxa**. Especially, geomorphological and rock-type richness had significant predictive power in the models. These results promote the inclusion of geodiversity information in threatened species conservation management.
3. **Geodiversity was a good predictor of vascular plants in environments with moderate and low human impact (independent contribution) and it correlated negatively with land-use intensity.** If the shared contributions are taken into account, geodiversity contributed to plant species richness especially in moderately and highly human-impacted environments. These results highlight the need for further exploration of geodiversity-biodiversity relationships in human-altered landscapes, which will become increasingly common in the future.
4. **Landforms increase biodiversity, with few exceptions.** For instance, gullies, river shores, kettle holes and lake shores were rich in alpha, gamma and beta diversity. The results of this thesis encourage exploration of multiple levels and measures of biodiversity and paying attention to landforms in nature conservation. As they are relatively easy to identify and map, this can be of great use, especially in planning local-scale conservation in specific areas.

5. **The results support the Conserving Nature´s Stage strategy.** According to the results, geodiversity seems to have a positive relationship with biodiversity. Geodiversity has an effect on biodiversity patterns at different areas and scales. Although geodiversity measures were not the strongest correlates of biodiversity, they had consistent positive relationships and increased species richness. In addition, biodiversity was often most pronounced on landforms. However, biodiversity correlated positively and geodiversity negatively with land-use intensity, reflecting a need for future studies to examine whether CNS is a valid principle in human-induced landscapes.

The main take-home messages for decision makers based on this thesis are:

- **Geodiversity should be incorporated in nature conservation management and decisions.** Not just for its own value (geoheritage and geoconservational value), but also because it supports biodiversity and could be used as a surrogate for measuring biodiversity.
- **Geodiversity could be used as a coarse-filter strategy for biodiversity conservation.** Geodiversity is a cost-efficient method to assess species distributions and may be helpful in situations where species data are limited or difficult to obtain. Geodiversity data can be used on its own, together with other abiotic data (such as climatic or DEM-based topographical data), or to complement species-level conservation.
- **Understanding the spatial distribution of geodiversity and how it is related to biodiversity can offer support for land management, sustainable exploitation of natural resources, and prioritization of conservation areas.**

Although an overall positive relationship between geodiversity and biodiversity in high-latitude environments was found in this thesis, more research is urgently needed to gain in-depth knowledge on the relationship at different geographical locations and spatial scales, and to inform appropriate ways of conserving nature in a holistic framework.

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