Maija Toivanen is a geographer who completed her PhD in the Geography Research Unit at the University of Oulu. Her dissertation focuses on geodiversity—the non-living diversity of nature, including rocks, soils, landforms and waters. While biodiversity and climate often dominate both academic and public discourse, Toivanen highlights the crucial role of geodiversity in these discussions. Her work provides both theoretical and methodological foundations for studying geodiversity, particularly in its relationship to biodiversity. Through her research, Toivanen encourages us to re-evaluate how we perceive natural diversity in our daily lives. It is often the mountainous landscapes and murmuring brooks that captivate us, revealing a hidden appreciation for geodiversity. By embracing a broader perspective on nature's diversity, we can foster a more holistic understanding and deeper appreciation of our natural world.

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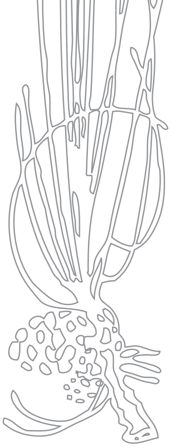

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Quantitative geodiversity assessment in biodiversity investigations

Maija Toivanen

Academic dissertation to be presented with the permission of the Doctoral Training Committee for Technology and Natural Sciences of the University of Oulu Graduate School (UniOGS) for public discussion in the lecture hall L10 on the 20th of September 2024 at 12.

Supervised by

Senior researcher
Janne Alahuhta
Geography Research Unit
University of Oulu
Finland

Professor
Jan Hjort
Geography Research Unit
University of Oulu
Finland

Postdoctoral researcher
Helena Tukiainen
Geography Research Unit
University of Oulu
Finland

Pre-examiners

Professor
Daniel Souza dos Santos
Institute of Geosciences,
Department of Mineralogy and
Geotectonics
University of São Paulo
Brazil

Researcher
Trond Simensen
Norwegian Institue for Nature
Research
Norway

Opponent

University lecturer
Sonja Kivinen
Department of Geographical and Historical Studies
University of Eastern Finland
Finland

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Contents

Appendices are available in the printed version of this publication.

Abstract

Despite the growing recognition of geodiversity in recent years, it remains overshadowed by its biotic counterpart, biodiversity. The objective of this thesis is to narrow this gap by advancing the quantitative assessment of geodiversity within the context of biodiversity. The main objective is to provide a theoretical and methodological framework for the study of landscape-scale geodiversity in biodiversity investigations, with some insights for nature conservation.

To achieve this goal, I will I) review the theory of the geodiversity–biodiversity relationship, II) empirically test the relationship in Finnish freshwater ecosystems, and III) provide data and methods for Europe-wide geodiversity and biodiversity studies. By employing quantitative geographical research methods inspired by ecological research traditions, I investigate the relationship between geodiversity and biodiversity across aquatic and terrestrial ecosystems.

Empirical investigations revealed positive correlations between geodiversity and vascular plant species richness in distinct studies conducted in Finland and Switzerland, across both aquatic and terrestrial ecosystems. This aligns with the theoretical assumption that geodiversity fosters greater biodiversity. Moreover, the Europe-wide geodiversity data produced within the thesis provides ready-to-use variables for future biodiversity investigations across the continent and contributes to large-scale geodiversity assessment in general.

In conclusion, I recommend further development of geodiversity assessment methods and the establishment of systematic frameworks for various research contexts. Such actions would facilitate the implementation of standardized and reproducible research practices, thereby helping to unlock geodiversity's potential in biodiversity and conservation research and in practice. Integrating geodiversity systematically into conservation and policy making is essential to fully acknowledge its crucial role in shaping sustainable future. By broadening perspectives on natural diversity beyond biodiversity alone, this thesis seeks to enhance general understanding and appreciation of geodiversity.

Keywords: geodiversity, biodiversity, georichness, species richness, quantitative assessment, GIS, nature conservation

Tiivistelmä (abstract in Finnish)

Geodiversiteetin käsitteen tunnettuus on viime vuosina kasvanut, mutta se jää yhä biodiversiteetin varjoon sekä tutkimuksessa että yleisessä keskustelussa. Tässä väitöskirjassa pyrin kuromaan umpeen käsitteiden välistä kuilua ja edistämään geodiversiteetistä käytävää tieteellistä keskustelua kehittämällä menetelmiä geodiversiteetin määrälliseen arviointiin. Tavoitteenani on tarjota teoreettisia ja menetelmällisiä lähtökohtia maisematason geodiversiteetin tutkimukseen, erityisesti biodiversiteetin tutkimuksen yhteydessä, ja samalla löytää luonnonsuojelua edistäviä sovelluksia.

Tavoitteen saavuttamiseksi I) teen katsauksen geodiversiteetin ja biodiversiteetin väliseen suhteeseen, II) testaan tätä suhdetta empiirisesti Suomen makeanveden ekosysteemeissä, ja III) tuotan geodiversiteettiaineiston sekä menetelmän ohjeistuksen geodiversiteetin määrälliseen arviointiin Euroopan laajuisia jatkotutkimuksia varten. Hyödynnän tutkimuksessani kvantitatiivisia maantieteellisiä ja ekologisia menetelmiä selvittääkseni geodiversiteetin ja biodiversiteetin välisiä yhteyksiä sekä vesi- että maaekosysteemeissä.

Empiirisissä tarkasteluissani havaitsin positiivisia korrelaatioita geodiversiteetin ja putkilokasvien lajirunsauden välillä eri tutkimuskohteissa Suomessa ja Sveitsissä, sekä vesi- että maaekosysteemeissä. Tämä tukee teoreettista oletusta siitä, että geodiversiteetti mahdollistaa rikkaamman biologisen monimuotoisuuden. Tuottamani Euroopan laajuiset geodiversiteettiaineistot tarjoavat valmiita ympäristömuuttujia tuleviin biodiversiteettitutkimuksiin eri puolilla Eurooppaa, ja edistävät maisematason geodiversiteetin arviointia ja mittaamista.

Tulosten perusteella suosittelen geodiversiteetin arviointimenetelmien jatkokehitystä ja systemaattisten tutkimuskehysten luomista eri tarkoituksia varten. Tällaiset toimenpiteet mahdollistavat standardoitujen ja toistettavissa olevien tutkimuskäytäntöjen kehittämisen, mikä puolestaan edesauttaa geodiversiteetin hyödyntämistä biodiversiteetin ja luonnonsuojelun tutkimuksessa ja käytännön toimissa. Geodiversiteetin systemaattinen sisällyttäminen esimerkiksi luonnonsuojeluun ja poliittiseen päätöksentekoon on välttämätöntä kestävän tulevaisuuden saavuttamiseksi. Tämä tutkimus laajentaa näkökulmia luonnon monimuotoisuuden tarkasteluun ja lisää yleistä ymmärrystä sekä arvostusta geodiversiteettiä kohtaan.

Avainsanat: geodiversiteetti, biodiversiteetti, georunsaus, lajirunsaus, määrällinen arviointi, GIS, luonnonsuojelu

List of original publications

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I Tukiainen, H., Toivanen, M. & Maliniemi, T. (2023). Geodiversity and Biodiversity. *Geological Society, London, Special Publications* 530: 31–47. https://doi.org/10.1144/SP530-2022-107

II Toivanen, M., Hjort, J., Heino, J., Tukiainen, H., Aroviita, J. & Alahuhta, J. (2019). Is catchment geodiversity a useful surrogate of aquatic plant species richness? *Journal of Biogeography* 46: 1711–1722. https://doi.org/10.1111/jbi.13648

III Toivanen, M., Maliniemi, T., Hjort., J., Salminen, H., Ala-Hulkko, T., Kemppinen, J., Karjalainen, O., Poturalska, A., Kiilunen, P., Snåre, H., Leppiniemi, O., Makopoulou, E., Alahuhta, J. & Tukiainen, H. (2024). Geodiversity data for Europe. *Philosophical Transactions of the Royal Society A* 382: 20230173. https://dx.doi.org/10.1098/rsta.2023.0173

Original publications are available in the appendices of the printed version of this thesis. Publication I is reprinted under CC BY 4.0 Creative Commons licence. Publication II is reprinted with permission from John Wiley and Sons. Publication III is reprinted under CC BY 4.0 Creative Commons licence.

Author's contributions

In Paper I, Tukiainen*, Toivanen and Maliniemi equally contributed to the research design and writing of the manuscript. Toivanen performed the initial literature review of the case studies to be included in the manuscript. Toivanen designed and lead the visualisation. Tukiainen as the lead author was responsible for the editorial communication and finalizing the manuscript for submission. *Tukiainen was appointed as a supervisor on 8 September 2023. Paper was first published 18 November 2022.

In Paper II, Toivanen, Alahuhta, Heino and Hjort designed the research. Toivanen performed the research, analysis, data processing, and visualisation. Tukiainen provided the geodiversity data, and Aroviita provided the river plant data. Toivanen was responsible for writing the manuscript, with supporting input from all authors.

In Paper III, Toivanen, Maliniemi, Hjort, Salminen, Alahuhta and Tukiainen designed the research. Toivanen performed the research, analysis, data processing, and visualisation. Toivanen led the data curation with supporting input from all authors. Toivanen was responsible for writing the manuscript with supporting input from all authors.

Acknowledgements

The journey of doing this PhD has been both challenging and rewarding, and now it is time to wrap it up and put a bow on it. At the beginning of my academic journey, I wasn't quite sure what to expect. If I had any expectations, they were likely not very realistic. In hindsight, having fewer expectations gave me freedom to explore. This freedom led me to pursue various—perhaps too many—opportunities and side tracks, but it also took my research in unexpected yet inspiring directions. The freedom to adapt my research plan based on my evolving interests and discoveries has been one of the most exciting aspects of this journey, and it has allowed my skills and confidence as a researcher to grow.

One thing I certainly did not expect was to undertake an additional master's degree while pursuing my PhD. However, studying science communication broadened my perspective on how to do research and, of course, how to communicate research.

I began my research with an intent to focus on freshwater ecology, but was a bit unexpectedly drawn to the topic of geodiversity. My background in geography, and later in science communication, provided a fruitful foundation for this shift. This background allowed me to take a broad perspective, draw inspiration from different fields and integrate various viewpoints. While the lack of specialisation sometimes feels frustrating and discouraging, especially in academia, I've come to appreciate the interdisciplinary nature and value of geography. Perhaps I will even continue specialising in geodiversity, spreading what I've come to describe as the "joy of geodiversity"—a phrase my colleagues and I have used whenever we've introduced the concept of geodiversity to someone new.

Of course, none of this would have been possible without the support of those around me. I would now like to acknowledge the many individuals and institutions that have supported and inspired me throughout this journey.

* * *

First of all, I would like to thank my supervisors, Janne Alahuhta, Jan Hjort and Helena Tukiainen. Janne, you believed in me and my abilities from day one and supported all my aspirations. My PhD journey has not been the most straightforward, but your conviction that a modern-day researcher should have a wide range of skills has allowed my journey to be so varied. Jan, you have played the many roles of professor, group leader, unit leader and supervisor during this long journey. Thank you for your expertise and patience along the way. Helena, although I only recently invited you to officially join my supervisory team, you have had the greatest impact on shaping my PhD research and inviting me into the world of geodiversity. You have always been such an encouraging and inspiring colleague, even before you became my supervisor. I have learnt so much from you, from organising files to leading projects. It is always an inspiration to work and discuss research with you.

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◆

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In addition to my thesis papers, I have been fortunate to work with many talented researchers on various projects. I'd like to thank everyone I've worked with over the past years on various research and science communication projects. In particular, I would like to thank Elina for fun writing experiences and giving me geological inspiration. I hope we can continue to work together in the future. I also want to thank Johanna and Helena for exciting discussions during our recent work project on nature-positive future. It is discussions like these that remind me why I love doing research.

Finally, not co-authors on paper, but equally important, were our FC Synopsis members. Marika, Marjo, Niina and Primi, you have had such an influence on my synopsis writing. We discussed writing, researching, structuring our synopses, but also created a safe space for feelings of failure and not meeting the expectations of ourselves or others. With you, I learned to write in baby steps. One sentence at a time, one paragraph at a time. Soon the baby steps turned into a complete manuscript. Thank you for reminding me to cherish all achievements, big and small.

◆

I would also like to thank my colleagues in the Geography Research Unit. Firstly, to the Physical Geography Research Group, thank you for all your support in the hard times and sharing joy in the happier times. We were a small group when I joined in 2018, but I've been lucky enough to see the group grow and get to know all the amazing people in it. Also, thank you Marja and Henriikka for letting me, an office PhD, join you on your fieldwork adventures in Tampere and Saariselkä.

Alongside the physical geographers, the collegial support of other researchers in the unit has been invaluable. Whether in the coffee room, at the pub or around the arts & crafts table. It always brings a smile to my face when I think of all the good times we have had together and the celebrations of many achievements.

Collegial support was also present in many unit and society activities. The Geographical Society of Northern Finland (PSMS) introduced me to scientific societies. Unfortunately, many small societies are struggling today, although they are valuable stepping stones and networks, especially for young researchers. Joining the Society for Regional and Environmental Studies (AYS) extended collegial support beyond the Geography Research Unit and the University of Oulu—and turned out to be one of the most rewarding events of my academic career so far. Firstly, I was able to develop my journal editing skills in a supportive environment. Secondly, I was taken out of my physical geography bubble and learned to appreciate the diversity of research—and research in the Finnish language. I would especially like to thank you, Minna, Ossi, Iina, Nina, Heikki and Senja. Working with you at Alue ja Ympäristö journal has been important and inspiring for me. I admire your skills and your ethics.

❧

As I mentioned before, my PhD journey was not the most straightforward. When I shake off the feeling of failing to meet external expectations, I can appreciate all the detours I took.

Firstly, the uncertainty of research funding led me to teach. And I am glad it did. Teaching GIS has made me a better and more confident researcher. Thank you Marjo, Harri and Terhi for all the fun times during the GIS courses. Working with you has made me feel valued and I have learnt a lot about both GIS and teaching from watching you. Thank you also to all the students. I've had many inspiring conversations and it is a joy to see your enthusiasm for geography (and geodiversity).

I was also lucky to get a one-year position in the GlobalFood project. Ossi, Terhi, Anita and Marton, working with you was the first time I had seen such a project working style. I learned a lot from all of you, and once again, felt safe and valued in the group. Thank you for the valuable research experience.

Another side track of mine was a bit longer one. Realising the importance of science communication in research (and the lack of it in research practice), I applied to study science communication at the University of Oulu. After starting my studies and struggling to twist my natural science brain to accept the reception of human science signals, I was swept away by the studies. In Tiema, we were a small group of students, and I'm afraid each of you got sick of hearing about geodiversity during our years together. But honestly, thank you for your company during our studies and the mental support, especially while writing our theses. I appreciate all the interesting discussions we had (and still have) together.

❧

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❧

I have been lucky to travel and meet other scientists at various geographical, biogeographical, ecological and geological conferences and other courses and events. Thank you for all the friendly encounters and stimulating discussions. And thank you to everyone at the Oulanka Research Station for always being the warmest place to retreat to.

I would also like to thank Richard Field and Franziska Schrodt for hosting my research visit to Nottingham, England—and all the other researchers I had the opportunity to meet during my stay. It was especially valuable to see the research environment outside the familiar Oulu bubble. And of course, in my free time I was able to explore the landscapes of the Peak District and the Lake District, which gave me new perspective on geodiversity. I hope my path will take me to the lakes again someday.

But, you don't always have to travel to be inspired by other researchers or research-minded. I would also like to thank everyone for their kind words online and on social media, which have given me unexpected encouragement and peer support.

❧

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1 Introduction

In year 2024, one can hardly argue that geodiversity is new term or concept. Nevertheless, it has yet to achieve the same degree of recognition as its biotic counterpart, biodiversity. The term ‘geodiversity’ was first introduced in the early 1990s as a response to the growing attention on biodiversity during the Rio Earth Summit in 1992. Geoscientists then argued that geodiversity, the non-living equivalent of biodiversity, is an equally diverse phenomena and important in conservation efforts (Gray 2021). However, the acknowledgment of the significance of the non-living environment predates this era. Geodiversity researchers today trace the recognition of the interconnectedness between abiotic and biotic environments back to the work of Alexander von Humboldt in the 1800s (Schrodt *et al.* 2019).

The number of scientific studies focusing on geodiversity began to increase significantly in 2010s. A total of 509 documents mentioning ‘geodiversity’ were recorded in Web of Science throughout the 2010s. By August 2024, the number of documents recorded in Web of Science since the beginning of the 2020s had reached 731, indicating a growing interest in the topic. Furthermore, geodiversity has gained wider public recognition in recent years, with UNESCO establishing International Geodiversity Day in 2021 (UNESCO 2022). This may also be a reason why Google stopped suggesting ‘did you mean biodiversity?’ when ‘geodiversity’ was typed into the search bar[1], making it easier for more people to explore geodiversity and all its wonders.

Increasing knowledge of geodiversity has led to the recognition of its various contributions to both nature and humans (Gray 2021). These contributions encompass a range of areas, including geosystem services, geomaterials, geotourism, geoheritage and geoconservation. Another contribution of geodiversity is that it underpins biodiversity. It has been suggested that a more diverse geological setting supports higher biodiversity, which is why geodiversity should have inherent conservation implications (Lawler *et al.* 2015). However, there is still much to clarify regarding the definition and measurement of geodiversity, as well as the study of its patterns and relationship with biodiversity in practical terms (Maliniemi *et al.* 2024). While the term ‘geodiversity’ is no longer new, its integration into practical actions and decision-making processes, and the interest in its relationship to biodiversity, are relatively recent developments.

This thesis is characteristic of geographical research, integrating insights from a range of disciplines, including geology and ecology. Geographical research involves the development of techniques to represent and manipulate spatial information across scales, encompassing both abiotic and biotic environments (Strahler 2013: 4–9). The subject of geodiversity presents a particularly intriguing area of geographical research due to its cross-disciplinary nature (see also Claudino-Sales 2021). While geological, pedological and hydrological maps are commonly produced in their respective fields, comprehensive geodiversity mapping remains relatively limited. Furthermore, this thesis explores the interconnections between geodiversity and biodiversity, drawing upon insights from ecological and biogeographical research that investigate the linkages and patterns between living and non-living environments (Kingsland 1991; Lomolino *et al.* 2016: 4–5). The diverse range of geographical research methodologies, including fieldwork, geoinformatics and statistical analysis, offers a versatile toolset for investigating geodiversity and the interrelations between the living and non-living environments.

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[1] This personal observation is based on search results in English. In Finnish, Google still suggests searching ‘biodiversity’ (*biodiversiteetti*) instead of ‘geodiversity’ (*geodiversiteetti*).

The objective of this thesis is to establish a conceptual and methodological framework for the study of geodiversity, with a particular focus on its application in the context of biodiversity investigations. This will be achieved by utilising quantitative data and methods derived from geographical, geological and ecological research. This thesis includes three original research papers, where I review the existing literature on the relationship between geodiversity and biodiversity (Paper I, Tukiainen *et al.* 2023), empirically examine this relationship (Paper II, Toivanen *et al.* 2019), and present Europe-wide geodiversity data and maps that facilitate broad-scale exploration of the geodiversity–biodiversity relationship (Paper III, Toivanen *et al.* 2024a).

First, I provide the theoretical background for the thesis. I present the research premise and central terminology for geodiversity (Chapter 2), summarise the quantitative research methods and trends in geodiversity assessment (Chapter 3), and provide more theoretical background on linking geodiversity to biodiversity (Chapter 4). After the theoretical section, I introduce more specific research objective and questions (Chapter 5), represent the used data and methodology (Chapter 6), followed by the main findings of the thesis (Chapter 7). Finally, I discuss the results in relation to past, current and future studies (Chapter 8) and conclude with both scientific and applied implications (Chapter 9).

2 Geodiversity

Geodiversity refers to the abiotic, or the non-living diversity of the Earth's surface and subsurface. It comprises of geological (rocks, mineral, fossils), pedological (soil), geomorphological (landforms, topography, physical processes) and hydrological features, including their assemblages, structures, systems and contributions to landscapes (Gray 2013). Geodiversity has numerous intrinsic, cultural, aesthetic, economic, functional and scientific values, one of which is that geodiversity provides foundation for biodiversity (Chakraborty & Gray 2020; Gray 2005). The heterogeneity in the non-living environment, created by both geodiversity and climate, essentially sets the stage for life to thrive (Anderson & Ferree 2010; Hjort *et al.* 2015).

Geodiversity is often overlooked in international conventions and policy discussions whereas biodiversity and climate are routinely included (Bailey *et al.* 2024). Given the equal significance of geodiversity as a component of natural diversity, there should be a similar interest in gathering information and improving our understanding on geodiversity, and its interconnections with biodiversity, climate and human activities. While considerable number of research has provided insights into biodiversity and its interactions with human activities and changing climates (IPBES 2019), geodiversity has not received the same level of attention.

To integrate geodiversity into research and policy discussions as routinely as biodiversity and climate, the development of a standardised terminology for geodiversity is essential. The following section will introduce the key terminology related to geodiversity within this thesis, which also establishes the methodological foundation for quantitative geodiversity assessment, which will be introduced in Chapter 3.

2.1 Geodiversity components

Geodiversity consists of four main components, including geological, pedological, geomorphological and hydrological diversity. Each of these geodiversity components holds a great variety of diversity, which can be viewed through different perspectives. As indicated in the definition of geodiversity, this variety can be explored in terms of the diversity of individual features, as well as the diversity in their structures or functions. Next, I will provide more detailed examples of how geodiversity can be viewed for each geodiversity component (Table 1). The examples primarily emphasise the varied contributions that each geodiversity component can have on biodiversity across scales.

From here on, 'geodiversity components' refer to geology, pedology, geomorphology and hydrology. Although these terms are distinct scientific disciplines, in this context, they are used to refer to the components of geodiversity, thereby simplifying the terminology for clarity. The individual features within each component are referred to as 'geofeatures' (e.g. a single soil type or landform). Notably, the term 'geodiversity element' is used synonymously with 'geofeatures' (see also Hjort *et al.* 2024).[2]

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[2] The term 'geodiversity element' was used to refer to geology, pedology, geomorphology and hydrology in Papers I and II. The terminology has been updated in Paper III and in the synopsis of the thesis, where I use the term 'geodiversity component' to refer to geology, pedology, geomorphology and hydrology. As the number of studies on geodiversity has grown rapidly, so has the terminology. The terminology used in this thesis synopsis aims to reflect the most commonly used terminology today.

Table 1. Geodiversity can be viewed from a number of different perspectives. In this table, examples are divided into three categories: compositional, structural and functional. These categories can be used in further geodiversity assessments.

	Geodiversity			
	Geological diversity	**Pedological diversity**	**Geomorphological diversity**	**Hydrological diversity**
Compositional perspective	Geological units (e.g. rock types)	Soil units (e.g. soil types)	Landforms	Hydrological features (e.g. wetlands)
Structural perspective	Geological heterogeneity (e.g. substrate heterogeneity)	Pedological heterogeneity (e.g. soil depth)	Topographical heterogeneity (e.g. terrain ruggedness)	Hydrological heterogeneity (e.g. surface moisture)
Functional perspective	Geological processes (e.g. evolutionary processes)	Soil processes (e.g. carbon cycle)	Geomorphological processes (e.g. slope dynamics)	Hydrological processes (e.g. flow dynamics)

Geological diversity is the variation in geological materials and processes, including rocks and sediments and materials (Gray 2013: 32; Hjort *et al.* 2024). Geological diversity can be considered as the variety of geological units (e.g. rock type) or their properties (e.g. composition or texture) (Table 1; Figure 1A–C). The classifications of rocks or sediments also embed information on the origins of the geofeatures. For example, surficial materials can be classified according to their formation, such as lacustrine or glacial deposits, or rocks can be classified according to the process by which they were formed, such as igneous or metamorphic rocks. Geological diversity can also be viewed through the lens of geological age. Geological age in relation to biodiversity can offer valuable insight into the co-evolution of geodiversity and biodiversity in landscapes (Read *et al.* 2020; Thomas 2012). Additionally, fine-scale geological features, such as fossils and minerals, contribute to geological diversity. They can have pronounced value in terms of geoheritage or their use as source materials for technology, respectively. It should be noted that the term ‘geodiversity’ is sometimes used as an abbreviation for ‘geological diversity’ especially in popular language (UNESCO 2023). However, here I consider ‘geological diversity’ as one component of geodiversity (sensu Gray 2013).

Pedological diversity encompasses the variation in soils, created by parent materials, climate, biota, topography and time (Gray 2013: 45–46; Jenny 1941; Figure 1D–F). Similar to geological diversity, soil diversity can be viewed as the variety in soil units, such as pedons (cf. soil classification system in United States Department of Agriculture 1999). Soils also have various physical, chemical and biological properties that contribute to soil diversity. Physical properties include texture, structure, density, porosity, consistence and colour, which in turn can be used in classifying soils into different types, such as sand or silt (cf. soil texture triangle in United States Department of Agriculture 2017). Chemical properties of soils are intricately linked to their capacity to support different organisms and ecosystems (Hulshof & Spasojevic 2020). In general, soils serve as an important abiotic–biotic interface, where separating the two is not always easy or even meaningful due to the diversity of life in soils and the fundamental role of biota in soil formation processes (Crowther *et al.* 2019). Therefore, exploring biological properties and processes, such as the nitrogen or carbon cycle, provides another dimension to understanding soil diversity (Table 1).

Figure 1. Visualisations of different geodiversity components, highlighting geological diversity (A–C), pedological diversity (D–F), geomorphological diversity (G–I), and hydrological diversity (J–L). Although geodiversity can be classified into different components, they all interact closely with each other. For instance, hydrological features and processes are evidently present in both geological, pedological and geomorphological diversity (A–I) and vice versa (J–L). Photos are from northern Norway (A, F–H), southern Germany (B), northern Finland (C–E, I–J, L) and southern Iceland (K). Photos: Maija Toivanen.

Geomorphological diversity includes variation in landforms and geomorphological processes, but also topography (Gray 2013: 12, 47; Figure 1G–I). From a global perspective, the predominant landforms are mountains, hills, plateaus and plains, collectively defining the terrain's topographical profile (Strahler 2013: 393). Since landforms often mirror the topographical profile, topographical heterogeneity could be used as a proxy for geomorphological diversity (Amatulli *et al.* 2020; Jasiewicz & Stepinski 2013; also at local scale as in Tukiainen *et al.* 2024). However, many more refined and distinct landforms appear at local scale, where also microtopography occurs across single landforms. Additionally, seemingly flat slopes can reveal significant heterogeneity via both fast (e.g. landslides) and slow (e.g. soil creep) slope processes. In contrast to many other elements of geodiversity, geomorphological processes, such as erosion, are highly dynamic. Geomorphology is a prime example of how geodiversity can occur both on long and short timescales, either as slow mountain building movements or sudden landslides.

Hydrological diversity includes variation in hydrological features, water chemistry, flow dynamics and surface moisture (Hjort *et al.* 2024; see also Alsbach *et al.* 2024; Figure 1J–L). Similar to geomorphological diversity, hydrological diversity can be understood as the variation in different features, such as lakes, rivers, or wetlands (cf. landforms), as well as from a process-oriented perspective through flow dynamics, such as flooding frequency (cf. geomorphological processes) (Table 1). Hydrological features can also be categorised based on their characteristics, such as lake area or shoreline length (e.g. in Polman et al 2024). Similar to pedological diversity and soil chemistry, water quality is equally a central aspect of hydrological conditions (e.g. white, black and clear river types in Alsbach *et al.* 2024), and consequently to aquatic life (Lacoul & Freedman 2006). Hydrological features and landscapes have not always been included in geodiversity definitions (see discussion in Gray 2013: 10–12). This is despite the fact that hydrology is intimately linked to other geodiversity components (see Figure 1). For instance, soil surface moisture can be considered as part of hydrological diversity. However, it very closely interacts with geomorphological processes (e.g. see calculations on topographic wetness index in Riihimäki *et al.* 2021).

Evident from above, geodiversity encompasses vast variety of natural diversity. While there is an overarching definition of geodiversity (as the diversity in geological, pedological, geomorphological and hydrological components), various perspectives can be adopted to explore the phenomenon. It can be a more compositional view, such as assessing geodiversity as the abundance of different rock units, soil units, landforms and hydrological features. On the other hand, one can view geodiversity from a more functional perspective, including aspects of temporal or process-based characteristics of each geodiversity component. While the definition of geodiversity is still evolving, it should always be clear how geodiversity is defined, in which context and why.

3 Measuring geodiversity

The definition of geodiversity is still evolving (Gray 2021). Thus, also the techniques to measure geodiversity are not yet established. The shared understanding is that geodiversity can be assessed either qualitatively or quantitatively (Zwolinski *et al.* 2018). Different methods are better suited for different purposes and different scales, but they can be also used together in joint qualitative–quantitative assessments to make the most of their best features, and to get complementary views on geodiversity. In this thesis, I focus on quantitative geodiversity assessment.

Quantitative methods are used to describe, for instance, the number of different geofeatures in a study unit. They are based on different data or numerical evaluations to produce geodiversity indices, and they require either measuring geodiversity in-situ or gathering, integrating and processing existing data. With quantitative methods it is possible to explore large geographical areas at once and cost-effectively, even in relatively small study units. As an example, a 2-m resolution digital elevation model is available for the entirety of Finland (National Land Survey of Finland 2024a). Quantitative assessments can also facilitate the allocation of more resource-intensive qualitative assessments by providing coarse or preliminary evaluations. In turn, qualitative methods can enhance the value of quantitative assessments by more accurately recognising regional features and their uniqueness, which is particularly beneficial for conservation purposes (see also Gonçalves *et al.* 2022; Tukiainen *et al.* 2024).

While numerous quantitative geodiversity assessment methods exist, they vary in their study objectives. Crisp *et al.* (2021) provide a summary of the current state of geodiversity assessment, noting that the majority of studies focus on geodiversity alone, although biodiversity is often discussed as a related topic. The increasing availability of data, particularly from remote sensing (RS) and geographic information systems (GIS), has facilitated methodological advancements. However, it has also resulted in a diverse range of approaches and data uses. The current challenge in quantitative geodiversity assessment is the lack of universal guidelines, as well as contradictions between quantitative and qualitative assessments and the underlying research motivations (see also Brilha 2015; Gonçalves *et al.* 2022).

This chapter begins by demonstrating how geodiversity assessment can benefit from decades of biodiversity research. It then introduces a quantitative assessment method that forms the basis of this thesis: a grid-based assessment system. As the focus of this thesis is on landscape-scale geodiversity, it concludes with a summary of what is meant by ‘landscape-scale’ in the context of geodiversity assessment in this thesis.

3.1 Inspiration from ecological research

The most common method for measuring biodiversity is to assess species richness. Correspondingly, geodiversity researchers have introduced the measure of ‘georichness’ to assess geodiversity (e.g. Bétard & Peulvast 2019; Hjort *et al.* 2022; Ruban 2010; Salminen *et al.* 2023; Tukiainen *et al.* 2017b; Tukiainen *et al.* 2024). Here, different ‘geofeatures’ or ‘geodiversity elements’ are considered as the abiotic equivalents of species. Individual geodiversity elements can be features such as rock types (e.g. granites), soil types (e.g. podzols), landforms (e.g. eskers), or hydrological features (e.g. ponds). Georichness is then calculated by summing up different geodiversity elements across a given area (Figure 2).

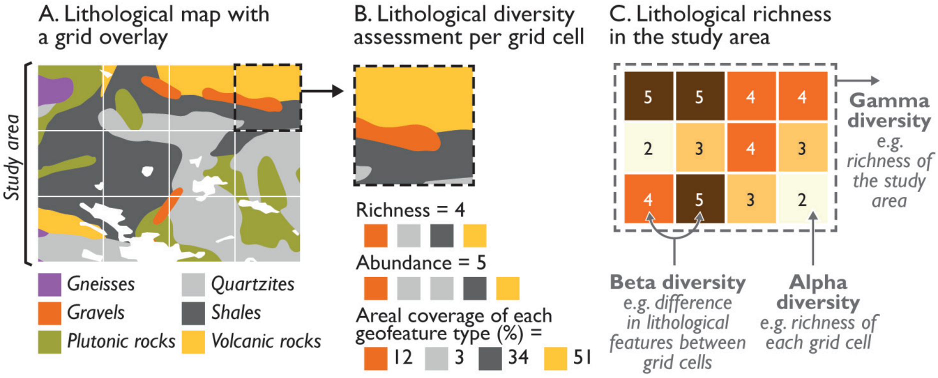

Figure 2. Schematic example of a quantitative assessment of geodiversity, using lithological diversity as an example. The assessment of lithological diversity can consider different characteristics, such as the richness of lithological features, the abundance of these features, or the area they cover within each study unit (A–B). This method allows for the production of diversity maps, as illustrated here with lithological richness (C). Additionally, other traditional methods of ecological diversity assessment, such as alpha, beta and gamma diversity, can be applied in the context of geodiversity (C). A compound geodiversity index would encompass geological (represented here as lithology), pedological, geomorphological and hydrological features. This approach is further illustrated in Figure 6. The lithological data in panel A is from Duscher *et al.* (2015).

Using georichness as a geodiversity measure can feel simplistic, compared to how many alternative perspectives there is to describe biodiversity in addition to species richness (see also Gray 2021 on quantitative geodiversity assessment). However, geodiversity research has certain practical limitations that make compositional diversity measures, such as georichness, more approachable than for instance functional diversity measures—especially investigated over larger spatial extents.

Until recently, geodiversity did not have a comprehensive taxonomy that would allow consistent assessment of geodiversity (see Hjort *et al.* 2024). Some taxonomies for different geodiversity components are well established, such as the World Reference Base for soils (IUSS Working Group WRB 2022), and major efforts have also been made to harmonise regional data to produce continental data products (e.g. European hydrogeology in Duscher *et al.* 2015). In addition, individual classifications have been developed for individual geodiversity components (e.g. hydro-geodiversity in Perotti *et al.* 2019 or landform-taxonomy in Ferrer-Valero *et al.* 2019), their combinations (e.g. rocks, landforms and soils in Bradbury 2014), or other characteristics (scale-based classification of geofeatures in Pellitero *et al.* 2015). However, a universal and harmonised geodiversity taxonomy (cf. biological taxonomy) for each geodiversity component would allow geodiversity to be explored in a comparable way with different diversity measures and across spatial and temporal scales.

A universal geodiversity taxonomy, as proposed by Hjort *et al.* (2024), would also allow the application of more advanced methods, such as functional geodiversity assessment, where geofeatures are classified based on their individual physical, chemical, morphological or temporal characteristics. In biodiversity research, measures of functional diversity are considered better indicators for assessing and conserving ecosystem functions than compositional measures such as species richness (Díaz *et al.* 2007, 2016). While such extensive information on individual geofeature properties does not exist yet that could be translated into 'functional traits' of geofeatures (cf. species trait databases such as TRY, https://www.try-db.org), the ideas are being developed. Lausch *et al.* (2024) recently presented how both vegetation and geodiversity related traits or characteristics can be monitored simultaneously with RS methods to support holistic ecosystem monitoring. On the other hand, functional geodiversity has also been linked to ecosystem services, where the categorisation is based on socio-ecological values of geodiversity (e.g. Scammacca *et al.* 2023).

There are also other examples of studying geodiversity using traditional measures and methods of ecological diversity. Already in the 1990s, pedologists used ecological diversity indices such as Shannon and Simpson to study soil diversity patterns (Ibáñez *et al.* 1995, 1998). Later, these indices were integrated into geodiversity assessments (e.g. Benito-Calvo *et al.* 2009) using methods from landscape ecology research (McGarigal *et al.* 2002). More recently, the concept of different levels of diversity—as alpha, beta and gamma diversity (Whittaker 1960, 1972)—has been demonstrated in the context of geodiversity (Tukiainen *et al.* 2023; see also Figure 2C). Adopted from assessing species diversity, one might be interested in the geodiversity within a certain location (alpha diversity), or the differences in geodiversity between two places (beta diversity), or the geodiversity across a region or landscape (gamma diversity). Georichness can describe either alpha (geodiversity in one location) or gamma (geodiversity across region) diversity (Figure 2C). Similarly, Erikstad *et al.* (2022) used principal component analysis to analyse similarities and dissimilarities between landscape units (cf. beta diversity).

3.2 Grid-based assessment

One method for quantitative assessment of geodiversity is to use a grid-based approach. According to the review by Crisp *et al.* (2021), it is the most used spatial assessment technique on quantitative geodiversity assessment. In the grid-based approach, the study area is divided into spatial units of equal size on which different diversity measures can be calculated (see Figure 2). It can be a simple georichness measure, where different types of geofeatures are summed within each grid cell (e.g. Tukiainen *et al.* 2017b), or a more complex geodiversity index, such as combining the richness approach with other parameters (e.g. Hjort & Luoto 2010), or calculating partial indices for different geodiversity components to produce a compound geodiversity index (e.g. Pereira *et al.* 2013). The previously mentioned alpha, beta and gamma diversity indices (Tukiainen *et al.* 2023) and other ecology-derived indices (e.g. 'geodiversity uniqueness' in Alahuhta *et al.* 2024) can also be applied to the grid system.

Many environmental variables used to explain biodiversity are often derived from grid-based data such as topography (Amatulli *et al.* 2020), land cover (European Environment Agency 2020) or climate (Karger *et al.* 2021). Grid-based methods are also mundanely used in biodiversity assessments and monitoring (e.g. Jetz *et al.* 2019; Lahti & Lampinen 2022). Therefore, grid-based methods enable fruitful premise for studying not only the relationship between geodiversity and biodiversity but also their interplay with climate and land use across large spatial extents. If grid-based surveys are longitudinal, temporal studies can also be conducted reliably.

Grid-based assessment is considered as a relatively objective survey method, and it can be used from local to global scales. Systematic grid assessment allows large areas to be surveyed at once, with equally sized survey units with systematic spatial coverage. It also allows for further analysis and sampling. Large-scale grid data are useful for identifying and explaining patterns across regions, which is often of interest in biogeographical or macroecological research (cf. Cervellini *et al.* 2020; Wüest *et al.* 2020), but also in nature conservation and land management (e.g. Underwood *et al.* 2018). Countries and continents also have systematic sampling grids for environmental surveys and monitoring (e.g. European Environment Agency 2013; Finnish Biodiversity Information Facility 2024). They allow data to be continuously updated and make different data compatible with each other.

The essential 'issue' or feature of grid-based assessment is the size of the grid cell (Hengl 2006), which is related to the Modifiable Areal Unit Problem or MAUP (Wong 2009). The size of the grid cell must be appropriate to the phenomenon under investigation. In geodiversity assessments, the choice of scale can be particularly difficult given the different characteristics of individual geodiversity components. For example, lithological features can be very large, while some hydrological features can be very small. Geofeature sizes also vary within a single component: some geomorphological features are very large, such as eskers, while others are much smaller, such as kettle holes in those eskers. Tectonic movement, on the other hand, can create both micro- and macro-scale fractures. Thus, the appropriate grid resolution is context dependent and can be based on cartographic features, but statistical methods can also be used to aid decision making (see Lopes *et al.* 2023; Polman *et al.* 2024). Additionally, the taxonomic level between geodiversity components and geofeatures should be coherent for the spatial assessment to be meaningful (see also Hjort *et al.* 2024).

3.3 Landscape-scale geodiversity

Geodiversity exists at all scales, from local to landscape to global, and can be linked to biodiversity at all these scales. In this thesis, I focus on landscape-scale geodiversity, a term that may seem rather vague. By definition, a landscape is '*all the visible features of an area of land, often considered in terms of their aesthetic appeal*' (MOT Oxford Dictionary of English 2024). Landscape doesn't have an exact spatial extent, but it rather refers to the motives and objects of the study. Landscape studies are usually interested in identifying patterns, interactions and processes over large extents, either from a society-centred or ecology-centred perspective, in both of which heterogeneity is key (see e.g. Wu 2006, 2013). Landscape studies, such as landscape ecology, increasingly rely on the analysis and synthesis of environmental information with various RS and GIS data (Wu 2013).

By 'landscape-scale' in this thesis, I refer to the spatial resolution of grid-based geodiversity assessments, which are 1-km and 10-km. The motivation for the study is to quantify geodiversity over large extents and relate the information to patterns of biodiversity. In addition, the geofeatures of interest (e.g. lithological units across Europe) and the data used (from national to global datasets) are best suited to observation at this scale. Resolutions from 1-km to 10-km also allow the assessment of geodiversity across different regions and scales, from watersheds to countries and continents (Figure 3), and are widely used in different geodiversity studies (e.g. Araujo *et al.* 2017; Lopes *et al.* 2023; Polman *et al.* 2024; Zarnetske *et al.* 2019).

Interestingly, 'landscape' has appeared in many earlier definitions of geodiversity, as discussed by Gray (2013: 10–11). Some of these restrict the definition of geodiversity to describing the variability of the abiotic environment of a particular landscape or limited area (e.g. Brocx 2008; Johansson 2000; Semeniuk 1997), in contrast to the idea of geodiversity is an overarching term for abiotic natural diversity, such as biodiversity is for biotic diversity. Michael Stanley (2004) also emphasises the role of geodiversity in the links between humans, landscapes and culture. In the most widely used definition of geodiversity by Gray (2013), geodiversity includes the 'landscape contributions' of different geological, pedological, geomorphological and hydrological components. My interpretation of landscape contributions is that it incorporates the functional perspective of geodiversity into the definition, recognising the central role of geodiversity in shaping the environment. It also emphasises the aesthetic appeal and value of geodiversity, which is most visible in landscapes.

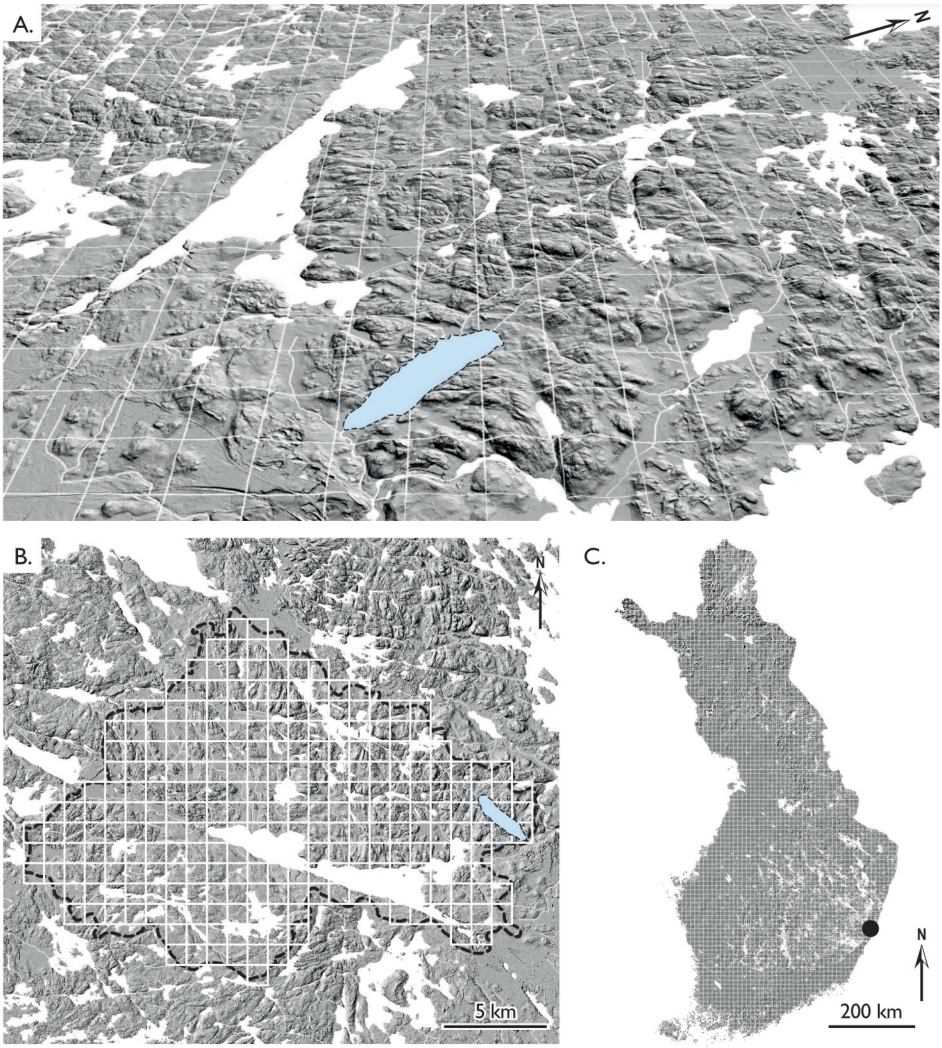

Figure 3. Grid-based landscape-scale assessment of geodiversity. Illustration of a grid overlay on a 3D landscape image (1-km grid; A), applied to a catchment area (1-km grid; B), and applied at a national scale (10-km grid; C). Both the 1-km and 10-km grids are based on the reference grids of the European Environment Agency (2013). The location of the visualized catchment in panels A and B is Lake Silamus in Rautjärvi, Finland. Background maps are from the National Land Survey of Finland (2024b; hillshade image in panels A–B) and the European Environment Agency (2016; DEM-derived hillshade image in panel C). Lake and river data are from the Finnish Environment Institute (2021).

4 Linking geodiversity and biodiversity

Studying the link between the living and non-living nature traces back to the era of Alexander von Humboldt (1769–1859) and beyond (Schrod *et al.* 2019). Modern ecological research has always included aspects of the abiotic nature—studying organisms and their interactions with one another and their physical environment—although the emphasis within its definition has varied over time (Cary Institute 2024). However, ecological research often tends to be biocentric, focusing primarily on the study of living diversity, which is understandable given its foundation as a sub-discipline of biology. This biocentric perspective can sometimes lead to a neglect of the intrinsic value and importance of geodiversity (see also Fox *et al.* 2020; Gray 2008a). Therefore, there is a need for complementary approaches to explore the relationship between biotic and abiotic diversities.

Gray (2021) argues that empirical interest in studying the link between geodiversity and biodiversity sparked with studies of geomorphological heterogeneity and its contribution to biodiversity (Burnett *et al.* 1998; Nichols *et al.* 1998). Since then, the concept has evolved and expanded to include more diverse views of geodiversity (e.g. Antonelli *et al.* 2018; Bailey *et al.* 2017; Hjort *et al.* 2012; Parks & Mulligan 2010). With an increasing number of case studies on the contribution of geodiversity to biodiversity, the conceptual framework for geodiversity–biodiversity relationship is starting to take shape.

In this chapter, I will first introduce the basic links between geodiversity and biodiversity and some theoretical background for geodiversity–biodiversity research. Because my thesis includes empirical testing in both aquatic (Paper II) and terrestrial (Paper III) environments, I also discuss geodiversity assessment in both environments.

4.1 Geodiversity and biodiversity in landscapes

Geodiversity, like biodiversity, exists at all scales. Tukiainen, Bailey & Hjort (manuscript) distinguish four fundamental links between geodiversity and biodiversity. These are: geodiversity providing settings for evolution, basic factors for life, places for organisms and shelter and protection. While nutrient and soil properties are important contributors to biodiversity at smaller scales, continental features, such as mountain ranges, determine life at the continental scale. In between at the landscape-scale, geodiversity consists of range of rocks, soils, landforms, hydrological features and related processes, that create varying spaces for species to occupy (Figure 4).

At all scales, geodiversity is intimately linked to water, nutrients, energy and space, which are considered to be the primary drivers of biodiversity (Field *et al.* 2009; Parks & Mulligan 2010). Geological, pedological, geomorphological and hydrological features and processes, for instance, moderate the water cycle, store and provide nutrients, regulate energy (e.g. via topography) and add complexity to abiotic environments (Tukiainen, Bailey & Hjort, manuscript; Lawler *et al.* 2015).

In this thesis, my focus is especially on the landscape-scale geodiversity. The contribution of geodiversity at landscape scale is most evident in abiotic heterogeneity that creates niche space for species through different geological, pedological, geomorphological and hydrological materials and processes.

Many of the examples from recent and more distant history show that landscapes and larger-scale processes have inspired much of the integration of geodiversity and biodiversity. The interconnectedness of abiotic and biotic nature was at the heart of the work of the botanist and geographer von Humboldt, who was particularly fascinated by altitudinal and latitudinal gradients of diversity (Norder 2019). Also, his successor Charles Darwin (1809–1882), best known for his theory of evolution, was inspired by the contribution of Earth's dynamic processes to species (Bressan 2012).

The relationship between geodiversity and biodiversity can also be contextualised within the framework of more contemporary ecological theories. At the landscape level, the environmental heterogeneity theory suggests that the relationship between geodiversity and biodiversity is positive due to environmental heterogeneity (Schulze *et al.* 2019: 769; Stein *et al.* 2014). The intermediate disturbance hypothesis (e.g. Connell 1978) can also be linked to environmental heterogeneity as it focuses on the spatial and temporal variation in environmental conditions. While many geodiversity components and geofeatures are considered stable, some abiotic processes create (natural) disturbances that promote species and community diversity (e.g. Viles *et al.* 2008; Virtanen *et al.* 2010). For instance, in riverine landscapes, several fluvial processes occur that structure diversity patterns across the aquatic–terrestrial ecotone, such as erosion, transport and deposition of materials (e.g. Ward *et al.* 2002). However, these theories derive from a bio-ecological perspective.

Figure 4. Geodiversity and biodiversity in the landscape. Different components of geodiversity are especially distinguishable in barren landscapes, such as in this one in northern Sweden. The topographic profile, shaped by the region's geological characteristics and geomorphology, creates vegetation gradients. On steep slopes, weathering can be a disturbance for species, but the diverse array of geomorphological features and processes also fosters habitat diversity in landscapes. Soils are an important abiotic–biotic interface, although they are susceptible to various forms of erosion. Hydrological features provide habitats for wetland and aquatic species, and important sources of water for both wildlife and passing hikers. Hydrological processes also shape landscapes from icy mountaintops to underground. Photo: Maija Toivanen.

Relatively more emphasis is placed on the non-living environment in the field of biogeomorphology, which studies the interactions between landscape dynamics and organisms. Biogeomorphology emphasises the two-way interaction between the living and the non-living. It also considers how global change affects not only species but also the non-living environment (e.g. Viles & Coombes 2022). This highlights the importance of studying natural systems as a whole, including both the ecological communities and the abiotic systems, and giving them equal attention. Viles & Coombes (2022) also stress that changes in both biotic and abiotic systems lead to changes in ecosystem processes and functions, which in turn affect the services humans receive from nature.

The geophysical environment has fascinated researchers and conservationists as a long-term conservation opportunity to protect both geodiversity and biodiversity simultaneously (e.g. Anderson & Feree 2010). Advancing technologies and increasing data have made even remote parts of the globe accessible, increasing the attractiveness of geodiversity as a proxy for biodiversity and as a coarse-filter conservation strategy. This is an often cited idea and motivation behind various geodiversity research, also known as the Conserving Nature's Stage, where geodiversity is considered as a stage of nature and species as actors (Anderson & Feree 2010; Beier *et al.* 2015 and articles in the special issue; Hunter *et al.* 1988). According to this strategy, conserving the stage (i.e. geodiversity) is expected to simultaneously protect the actors (i.e. biodiversity), especially in the context of climate change, by preserving refuges for species (Lawler *et al.* 2015).

Similar approaches with conservation intentions are found in various methods, such as land facets (or recurring landscape units) that are used to complement biocentric management plans (Brost & Beier 2012), or geo-ecology that integrates both geodiversity and climate considerations (Gordon *et al.* 2001; Hugget 1995). Thus, the idea of using abiotic nature or geodiversity as a tool in conservation efforts is not unique, and there are many examples beyond those mentioned above, but it lacks a universal basis and tools on which to build.

4.2 Geodiversity in terrestrial and aquatic environments

Geodiversity exists and underpins biodiversity in all types of environments and at all scales, including terrestrial, freshwater and marine ecosystems. When studying the relationship between geodiversity and biodiversity, geodiversity should be considered in the context of the environment and the context in which the geological, pedological, geomorphological and hydrological features are studied.

In general, terrestrial environments have been studied more intensively in geodiversity–biodiversity research than freshwater or marine environments (Alahuhta *et al.* 2020; Crisp *et al.* 2021). Terrestrial environments are more accessible to study both in situ and remotely, which can easily lead to empirical bias in research efforts. In contrast, aquatic environments tend to require more resources to study. While environmental variability in terrestrial environments, such as topography or soil properties, can be studied intensively, we don't have similarly comprehensive and accurate information on subsurface topography (e.g. depth gradients) or soil (or sediment) properties—or on other geodiversity components either.

Even though I am making a distinction between terrestrial and aquatic environments here, they are not completely independent of each other. For example, lakes and rivers are linked to the materials and processes that occur in their catchments (Heino *et al.* 2021; Soininen *et al.* 2015). While the physical properties within the lake play a key role in shaping the aquatic communities, the various natural and anthropogenic processes and activities in the catchment also influence the environmental conditions (and thus the biological communities) within a lake or river (Johnson *et al.* 1997; Lacoul & Freedman 2006). The interconnectedness of ecosystems is also present in the Conserving Nature's Stage concept, where the idea is to conserve large abiotic regimes. Thus, also conservation and restoration efforts should consider whole catchments, including both terrestrial and aquatic habitats.

Grid-based assessment methods (introduced in Chapter 3) are likely to be more useful in landscape-scale studies and in spatially continuous terrestrial environments than at a more local scale in lakes or rivers, which have a network structure (cf. Moilanen *et al.* 2007 on conservation prioritisation methods in freshwaters). While the grid-based approach is applicable to freshwater catchments (Figure 3), the study of the water bodies themselves may require different types of approaches for biodiversity and geodiversity assessments (Figure 5). For both lakes and rivers, a variety of standardised biodiversity assessment methods exist (e.g. Brucet *et al.* 2013). However, there are also some standardised survey methods designed to investigate the abiotic diversity in freshwater environments, such as the Europe-wide River Habitat Survey (Raven *et al.* 1998). The River Habitat Survey accounts for various geodiversity components, and it also takes into account the specific characteristics of fluvial landscapes, such as flow dynamics or riparian features within the survey site. The approach has already inspired local-scale geodiversity investigations (Stefanidis *et al.* 2023; but see also Kärnä *et al.* 2018), and could be further applied in the development of local-scale geodiversity assessment methods for riverine environments.

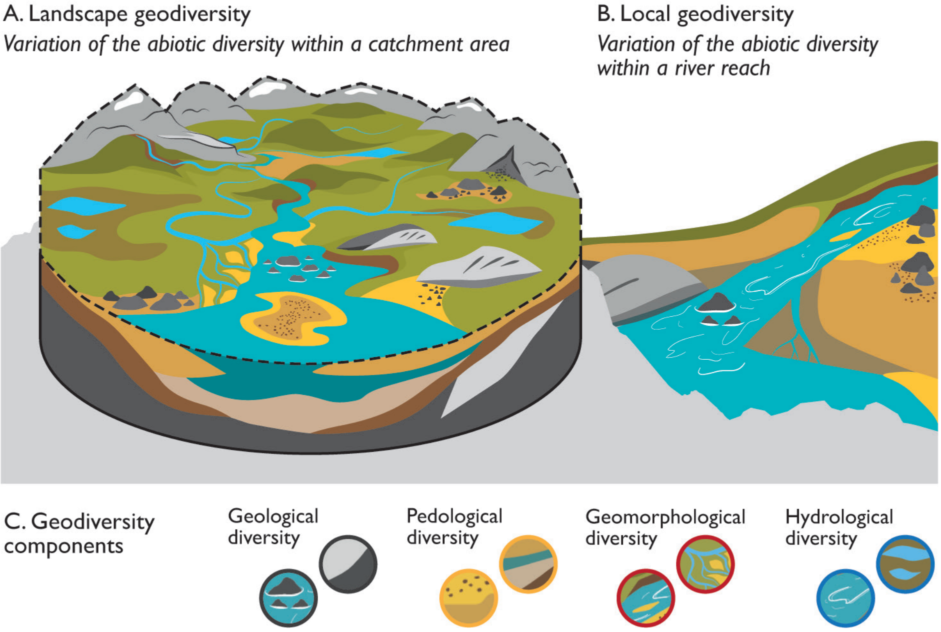

Figure 5. Schematic representation of freshwater geodiversity. Geodiversity and its different components exist at all scales, although they may need to be assessed differently in different contexts. For instance, hydrological diversity within a catchment area can be quantified as the presence of hydrological features or habitats (e.g. Tukiainen *et al.* 2017a). At the local scale, hydrological diversity can be assessed as variation in flow types (e.g. Kärnä *et al.* 2018).

Over the years, a few marine geodiversity assessments have emerged, for example in the Baltic Sea (Kaskela & Kotilainen 2017, 2024), Hawaii (Seijmonsbergen *et al.* 2018) and Norway (Dolan *et al.* 2022), using a grid-based approach familiar from many terrestrial geodiversity studies. While all of these studies note that the availability and accuracy of data on marine geodiversity components hinders comprehensive assessments, particularly over large contiguous areas (see also Costello *et al.* 2018), the resource-intensive nature of biodiversity surveys in remote underwater environments highlights the great potential of geodiversity to advance our understanding of natural diversity in marine environments (cf. Kaskela *et al.* 2017).

Although geodiversity should be considered differently in different ecosystems, standardising geodiversity in geodiversity–biodiversity surveys would advance our understanding of how they are connected across ecosystems (see also Maliniemi *et al.* 2024). More specifically, it would be important to consider all aspects of geodiversity (geological, pedological, geomorphological and hydrological diversity), even if the exact measures of geodiversity are not the same. However, using the same geodiversity data and methodology in both environments would allow better comparison and generalisation of results.

5 Aim of this thesis

The main aim of this thesis is **to provide theoretical and methodological premise to study landscape-scale geodiversity in relation to biodiversity**. To do this, I review the current understanding of the relationship between geodiversity and biodiversity, test the relationship empirically, and provide tools for further Europe-wide geodiversity and biodiversity research. Finally, I discuss the potential and limitations of geodiversity–biodiversity research for scientific and applied implications. More specific research objectives are divided based on the original research articles Paper I (O1), Paper II (O2) and Paper III (O3) with individualised research questions (RQ1–RQ6).

O1 To review the current understanding and knowledge gaps of geodiversity–biodiversity research

The main objective of Paper I was to summarise the current understanding of research on the relationship between geodiversity and biodiversity. The increase in geodiversity –biodiversity studies over the last 10–15 years has resulted in diverse research, for instance in terms of geodiversity assessment methodologies. By reviewing the current status, we can better guide future research on the geodiversity–biodiversity relationship, and to point out the knowledge gaps in empirical research, such as bias in spatial scales, ecosystems or taxa—but also conceptual and methodological gaps in geodiversity research and assessment. In the context of this thesis, I am especially interested in:

RQ1 How does current empirical evidence support the theoretical background of geodiversity–biodiversity relationship at landscape-scale?

RQ2 What are the methodological gaps in geodiversity assessment in biodiversity investigations?

O2 To empirically test the geodiversity–biodiversity relationship in freshwater ecosystems

In Paper II, I focus on the less studied freshwater ecosystems and investigate the relationship between catchment geodiversity and aquatic plant species richness. Previously, a corresponding grid-based geodiversity assessment in terrestrial ecosystems has proven useful for investigating the relationship between geodiversity and vascular plant diversity and other taxa (e.g. Hjort *et al.* 2012; Tukiainen *et al.* 2017a, 2017b). Here, I use a similar geodiversity dataset to enable comparability and to assess the applied potential of the geodiversity data based on a grid-based assessment method. Repeated empirical evidence of the positive relationship between geodiversity and biodiversity (especially across ecosystems) would encourage testing the relationship elsewhere. However, further studies would require consistent methodology and geodiversity data beyond regional and national assessments. In order to achieve this goal and to support further empirical research, I am asking:

RQ3 How are geodiversity and biodiversity linked in freshwater ecosystems?

RQ4 Is grid-based geodiversity assessment suitable for biodiversity investigations in freshwater ecosystems?

O3 To provide tools for Europe-wide geodiversity–biodiversity research

In Paper III, I aim to establish and provide standardised research methods and data to advance empirical research on geodiversity and biodiversity. Through literature review and empirical testing, a grid-based geodiversity assessment method has shown potential to elucidate the relationship between geodiversity and biodiversity and provide a better understanding of their interconnections. With Europe-wide data, researchers with specific area or taxa expertise can engage in the empirical studies required in this niche of geodiversity research. My aim is therefore to address the following questions:

RQ5 How does the European geodiversity data contribute to quantitative geodiversity assessment?

RQ6 How can European geodiversity data be applied in biodiversity investigations?

6 Data and methods

In this chapter, I introduce the data and methods used in the thesis. First, I describe the Finnish and European geodiversity data featured in Papers II and III, followed by an overview of the grid-based geodiversity assessment method. After introducing the geodiversity assessment method, I describe how the data was applied in biodiversity investigations. More specifically, I introduce the species data and selection process used in both studies and explain how the geodiversity data was applied in the specific research. Finally, I describe the complementary environmental data and statistical methods used in the analysis. Paper I, as a review article, does not involve data analysis and is therefore not referenced in this section.

6.1 Geodiversity source data

Two different geodiversity data were used in this thesis. In Paper II, we used a Finnish geodiversity data which was originally compiled by Tukiainen *et al.* (2017a) and Tukiainen *et al.* (2017b) to study to the biodiversity–geodiversity relationship in Finland. In Paper III, we produced a new Europe-wide geodiversity data, but used both the Finnish and European geodiversity datasets in the research. The Finnish geodiversity data served as a benchmark to validate the new European dataset through correlation analysis. Both the Finnish and the European geodiversity data were used to demonstrate their use in the context of geodiversity–biodiversity research by correlating the variables of georichness and vascular species richness in two different study areas: Finland and Switzerland.

Both the Finnish and the European geodiversity dataset include four geodiversity components (geological, pedological, geomorphological and hydrological features) following Gray's (2013) definition of geodiversity. Notably, different names are used for those components in order for them to be descriptive of their content (Table 2). Both datasets provide extensive descriptions of abiotic feature richness, with the Finnish data recognising 37 geofeatures and the European data recognising 78 geofeatures. The source data for the European and Finnish datasets are independent of each other, with no overlap between geofeatures in their respective source data. The Finnish data are based on national datasets and the European data are based on European and global datasets. The European source data also have a coarser spatial resolution than the Finnish national source data (e.g. geological dataset scales of 1:1 500 000 to 1:200 000, respectively). The data sources are listed in Table 2, but more detailed descriptions are available in the original research papers (Finland in Tukiainen *et al.* 2017a, 2017b; Tukiainen & Hjort 2019; Europe in Paper III, Toivanen *et al.* 2024a).

Although the geodiversity components are similar in both datasets, there are differences in how geofeatures are classified into the geodiversity component categories or what they represent specifically. For instance, 'soil' and 'rock' in the Finnish dataset and 'geology' and 'pedology' in the European dataset are not fully comparable. Soil data in the Finnish data describes the superficial deposit types (such as till or silt) while pedology in the European data describes pedon types (such as histosols or gleysols) (see also the geodiversity taxonomy in Hjort *et al.* 2024). Lists of these individual geological and pedological geofeatures can be found in Paper II (Table S1.4 in Toivanen *et al.* 2019) and Paper III (Table S1.1 in Toivanen *et al.* 2024a). Geomorphology was also treated differently in these two datasets. In the Finnish data, geomorphological diversity is a modelled geomorphological richness variable based on landform observations,

Table 2. Summary of geodiversity source data and geofeatures. Geodiversity components and geofeatures are referred to with the same names than in their original research papers (Finland in Tukiainen *et al.* 2017a; Tukiainen *et al.* 2017b; and Europe in Toivanen *et al.* 2024a).

Geodiversity dataset	Geodiversity component	Geofeatures	Source data	Reference
Geodiversity, Finland[1]	Rock	Rock types (n=7)	Bedrock of Finland 1:200 000	Geological Survey of Finland 2010a
	Soil	Soil types (n=7)	Superficial deposits of Finland 1:200 000	Geological Survey of Finland 2010b
	Geomorphology	Geomorphological features (n=18)	Unpublished data	Tukiainen *et al.* 2017b
	Hydrology	Hydrological features (n=5)	Groundwater bodies	Finnish Environment Institute 2013
			Topographic database (wetlands)	National Land Survey of Finland 2012
			Water bodies (rivers)	Finnish Environment Institute 2015
Geodiversity, Europe[2]	Geology	Lithological classes (n=29)	IHME1500	Duscher *et al.* 2015
	Pedology	Soil (pedon) classes (n=28)	SoilGrids 2.0	Poggio *et al.* 2021
	Geomorphology	Terrain forms (n=10)	Geomorpho90m	Amatulli *et al.* 2020
	Hydrology	Hydrological features (n=11)	EU-Hydro (water bodies)	European Environment Agency 2019
			Corine Land Cover 2018 (wetlands)	European Environment Agency 2020
			IHME1500 (groundwater)	Duscher *et al.* 2015

1 For the full list of the soil and rock type names, see Paper II (Table S1.4 in Appendix 1 in Toivanen *et al.* 2019). Geomorphology is a modelled richness variable and individual geofeatures cannot be listed. Hydrological features include aquifers, wetlands, rivers, lakes and sea areas, but they were not included as geodiversity variables in Paper II where we studied the lake and river aquatic plants.

2 For full list of all geofeatures names, see Paper III (Table S1.1. in Appendix 1 in Toivanen *et al.* 2024a).

topographic variables and geographic variables (see details in Tukiainen *et al.* 2017b). The European data, on the other hand, use landform richness as a proxy for geomorphological diversity, where landforms describe the dominant landscape form (such as flat or slope area; Amatulli *et al.* 2020).

Despite the disparities between the datasets, both were compiled with practical applications in mind, focusing on their potential contributions to investigations of the relationship between geodiversity and biodiversity. Thus, the relevance of geofeatures to biodiversity was taken into consideration when selecting the original source data. Additionally, in line with the concept of geodiversity as encompassing the diversity of the Earth's (sub)surface abiotic nature, we aimed to incorporate a diverse array of geodiversity components. We also considered the diversity within the components, such as using various data sources to describe hydrological diversity. The Finnish geodiversity data was partly classified manually to emphasise the biological relevance of specific components, as the bedrock and soil types were reclassified (see Tukiainen *et al.* 2017b for more details). For European data, we used existing classifications or taxonomies for lithology and soils to support better applicability. The use of original classes improves the traceability of the data and facilitates potential reproduction.

In producing the European geodiversity data, we also emphasised the representativeness and the spatial and taxonomic accuracy of the source data. While we prioritised European data sources, we also used global data when they were considered sufficiently accurate. For example, when selecting the global SoilGrids as a source for soil data, we considered its widespread use in biodiversity studies (e.g. Antonelli *et al.* 2018), while also assessing its validity in Europe. The dense training data used in SoilGrids modelling increases its accuracy in this region. However, SoilGrids has also proved suitable for geodiversity assessments at a global scale (see Polman *et al.* 2024).

6.2 Grid-based geodiversity assessment

Both the Finnish and the European geodiversity datasets are based on GIS data, zonal calculations and a grid-based assessment method. While I focus here on describing the assessment process with the European geodiversity data, the same principle was followed with the Finnish geodiversity dataset (see details in Tukiainen *et al.* 2017a and Tukiainen *et al.* 2017b). The main principle of the grid-based assessment method is visualised in Figure 6.

Grid-based assessment requires a grid on which different indices can be calculated. For the European geodiversity data, we used a Europe-wide reference grid produced by the European Environment Agency (2013). The reference grid is available at various resolutions from 1-km to 100-km of which 1-km and 10-km resolutions were used here. 1-km and 10-km were chosen because they are suitable for capturing the diversity within individual geodiversity components (i.e. suitable for source data resolution). These specific scales have also been shown to be efficient scales for geodiversity assessment (e.g. Lopés *et al.* 2023; Polman *et al.* 2024). While the 10-km and coarser resolutions are readily available covering all Europe, the 1-km grid required merging the original reference grid country-by-country. The spatial extent of the European geodiversity dataset was based on the limiting extent of the Corine Land Cover data, which we discuss in more detail in Paper III (Appendix 2 in Toivanen *et al.* 2024a).

We used ArcGIS Pro software (version 2.8, Esri 2021) to produce the geodiversity data. However, the zonal analysis methods for calculating geodiversity variables are accessible and reproducible in various GIS and statistical software. Specifically, we used the ‘Zonal Statistics as Table’ tool to summarise the number of different geofeatures within each grid cell (Esri 2024a). This tool produced the measure of ‘georichness’. In addition, we used ‘Tabulate Area’ tool to calculate the areal coverage of each geofeature within each grid cell (Esri 2024b).

Grid-based calculations are relatively straightforward, although they still require careful data preparation. Details of the European data calculation are described in Paper III. Here I summarise some of the key steps in grid-based assessment pre-calculations (cf. Figure 6A–B).

After selecting the geodiversity source data, we checked for overlapping or irrelevant information within or between datasets. For example, from the geomorphology component, we removed ‘flat’ landforms that overlapped with lakes. All lakes were represented as flat in the Geomorpho90m data, which doesn’t describe the true terrain

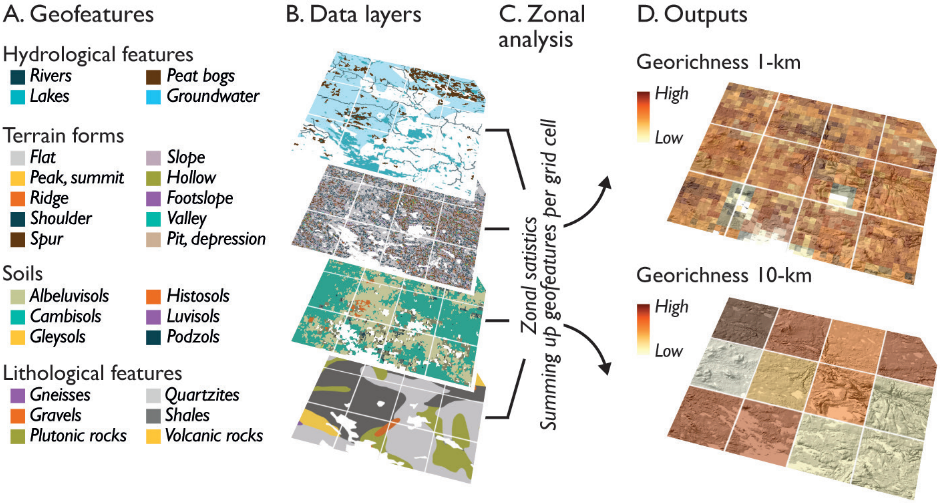

Figure 6. Visualisation of the grid-based geodiversity assessment method and process, including data selection (A), data preparation (B) and zonal analysis (C). The data illustrated in panel B are from Duscher *et al.* (2015; lithology, hydrology), Poggio *et al.* (2021; soils), Amatulli *et al.* (2020; terrain forms), and the European Environment Agency (2019, 2020; hydrology). The outputs display georichness variables, where distinct geofeatures were summed for each grid cell at 1-km and 10-km resolutions (D). The illustration is a subset from the geodiversity data presented in Paper III (Toivanen *et al.* 2024a), located in the Oulanka region, Finland. The background map in panel D is from the National Land Survey of Finland (2024b; hillshade image).

within the lakes. From the lithology component we removed ‘inland water’ and ‘snow and ice fields’. Inland waters overlapped with lakes in the hydrology component. Snow and ice fields were not considered to be relevant for biodiversity at this scale. These decisions were influenced by the accuracy of the lithological data, but also by the availability of more recent, detailed and biodiversity-relevant information on snow and ice fields (see e.g. European Environment Agency 2023).

After refining the source data, we harmonised the data format and resolution. All vector data were converted to raster format. The resolution of each data was considered on a case-by-case basis. Soil data was processed at its original resolution of 250-m and all other data was set to 100-m. In particular, vector data tend to be detailed, such as the river network used here (European Environment Agency 2019). Considering both reliable presentation and computational requirements, we chose a resolution of 100-m for all vector data conversions. Finer resolutions based on the minimum mapping units of the geofeatures were also considered, but discarded due to computational requirements and coherence of the overall geodiversity dataset (see also details on sourca data in Table S1 in Paper III, Toivanen *et al.* 2024a). The chosen resolution is particularly relevant for the calculation of the areal coverage of each geofeature per grid cell and should be taken into account in the further use of these data.

We also aimed to produce geodiversity data that describes the diversity of (semi-)natural abiotic diversity, which is why clearly anthropogenic features were excluded from the data. For example, the Corine Land Cover data includes ‘salines’ in the wetland category. We have removed this class as it refers to salt production areas that are under significant land use pressure. Providing data describing (semi-)natural abiotic diversity also allows further exploration of geodiversity in relation to land use in the future (see e.g. Ren *et al.* 2021; Tukiainen *et al.* 2017a).

6.3 Applying geodiversity and biodiversity data

Paper II focused on Finnish freshwater ecosystems and investigated the relationship between catchment geodiversity and aquatic plant species richness. We selected a geographically representative sample of Finnish lakes (n=145) and rivers (n=146) with systematically surveyed aquatic vegetation data that is maintained by the Finnish Environment Institute (Figure 7). The aquatic vegetation surveys follow the ecosystem-specific protocols for lakes (Leka *et al.* 2003) and rivers (Rääpysjärvi *et al.* 2016). The surveys were completed in 2006–2012 and 2009–2012, respectively. Due to these differences in the survey methods and timing, lakes and rivers were studied separately. However, aquatic plants were grouped within lakes and rivers according to their life forms as helophytes and hydrophytes following Toivonen & Heikkinen (1995) to represent their functional role in the ecosystem. We used presence–absence data of lake and river plant species in the statistical analysis to describe the helophyte species richness, hydrophyte species richness and total species richness.

Catchment areas for each lake polygon and river sampling point were delineated using online-based VALUE tool by the Finnish Environment Institute (https://paikkatieto.ymparisto.fi/value). Catchment geodiversity was then calculated from the 1-km resolution Finnish geodiversity data measured as soil-type, rock-type and geomorphological feature type richness. For each catchment area, we calculated the variation of geodiversity as the standard deviation of total georichness, soil richness, rock richness and geomorphological richness variables. We used those variables to correlate catchment

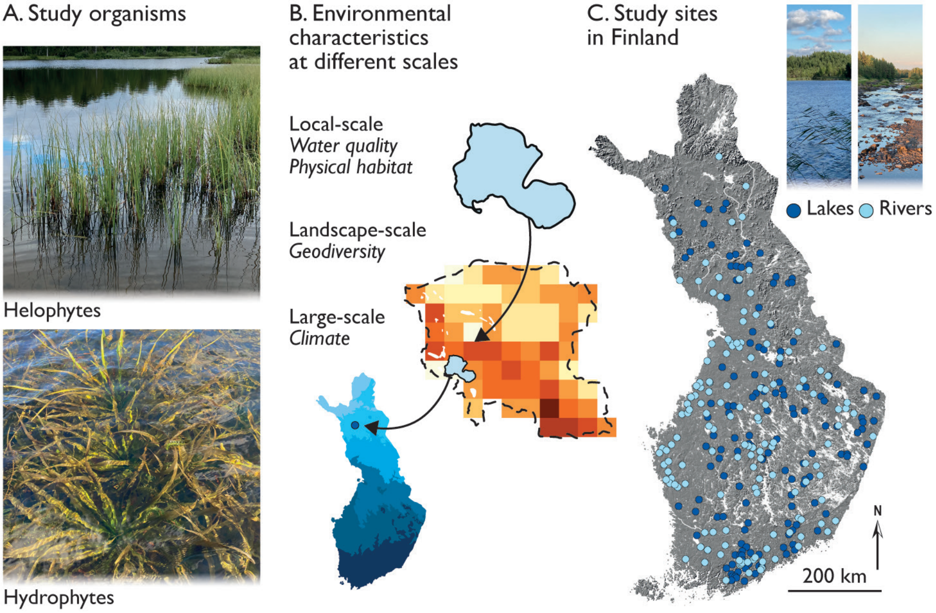

Figure 7. Study set-up in Paper II (Toivanen *et al.* 2019). Study organisms were aquatic plants, classified into helophytes and hydrophytes (A). We considered various characteristics as environmental variables. They operate at different spatial scales (from lake-level to catchment area scale and regional scales) and are relevant to freshwater ecosystems and biota (B). Study included 145 lakes and 146 rivers across Finland (C). Background map in panel C is from the European Environment Agency (2016; DEM-derived hillshade image) with lakes from the Finnish Environment Institute (2021). Photos: Maija Toivanen.

geodiversity with aquatic plant species richness and further investigate the geodiversity–biodiversity relationship with statistical techniques (described in the next sections).

Paper III focused on terrestrial ecosystems and investigated the relationship between georichness and vascular plant species richness in Finland and Switzerland. We used the open access biodiversity database GBIF (Global Biodiversity Information Facility) to obtain vascular plant species data from Finland (GBIF.org Finland 2022) and Switzerland (GBIF.org Switzerland 2022). More specifically, we used only one databank from each country to minimise the taxonomic and geographical biases known to exist in online databases, such as GBIF. 'Kastikka' databank was used for Finland (Finnish Biodiversity Information Facility 2023) and 'Swiss National Databank of Vascular Plants' databank was used for Switzerland (Jutzi *et al.* 2023). These data include all 'human observation' or 'preserved specimen' records of Tracheophyta species from 1985 to 2022. In both databases, species information was harmonised to species level, allowing a reliable assessment of species richness. Geographical bias was accounted for by manually cleaning the species data. In Finland, we selected species data only from those grid cells that were comprehensively mapped according to the Atlas of the Distribution of Vascular Plants in Finland (here at 10-km resolution; Lampinen & Lahti 2021). The species data in Switzerland have been mapped on a 5-km grid cell covering the whole country. Some deviating or insufficient data, especially along the edges of the data, were removed manually.

In Paper III, to explore the correlations between geodiversity and species richness, we calculated species richness variables for 10-km grid cells, corresponding to the 10-km European geodiversity study grid. In Switzerland, we summed the unique species in their respective 10-km grid cell and used the European geodiversity data at 10-km resolution as such. In Finland, we also explored the link with the Finnish geodiversity dataset, which is originally only available at 1-km resolution. Thus, we calculated mean richness variables to match the European geodiversity 10-km study grid from all 1-km resolution data: species richness, Finnish geodiversity and European geodiversity data. We chose the 10-km resolution to ensure comparability between the datasets. The accuracy of both species and geodiversity data was not sufficient to make a reliable comparison at 1-km resolution.

6.4 Other environmental data

In Paper II, we used complementary environmental data alongside geodiversity to better understand the role of geodiversity in investigating biodiversity patterns (Figure 7). For example, aquatic plants have been studied in relation to environmental conditions such as water quality or climatic conditions. We wanted to introduce geodiversity into this explanatory variable mix and see how geodiversity variables relate to more commonly used explanatory variables. Here, water quality and physical habitat characteristics were considered to operate at a local scale, whereas climate variables operate at a larger scale (Figure 7B). To account for the in-between landscape-scale, we incorporated catchment geodiversity to complement these more widely investigated environmental variables. Of local variables, we considered alkalinity and habitat size (i.e. lake area or river width) in the final analysis. Of larger scale climatic variables, we included growing degree-days (i.e. the annual temperature sum above 5 ºC) in the final analysis. Both the climatic and geodiversity variables were calculated for the lake or river catchment areas. For geodiversity variables, the standard deviation was used to describe abiotic heterogeneity in the catchments, and for climate variables, the mean was used to describe average conditions.

Water quality variables were averages of multiple samples taken during the growing season between 2006–2012 for lakes and 2009–2012 for rivers (i.e. the same years as the plant surveys were carried out) retrieved from the Hertta database (Finnish Environment Institute 2016/2024). Lake surface area was delineated from GIS data and river channel width was measured during the plant surveys. For the growing degree-day variable, we used climate data from the Finnish Meteorological Institute for the most recent normal period 1981–2010 (Pirinen *et al.* 2012). Other environmental variables were also considered but not included in the final analysis, such as total phosphorus and water colour. These are described in more detail in Paper II.

6.5 Statistical modelling

In Paper II, we used statistical modelling to investigate the relationship between catchment geodiversity and aquatic species richness. We used a number of different, complementary modelling techniques to get a better overall picture of geodiversity variables in relation to the more commonly used environmental variables (i.e. local and climate). Our aim was to explore the potential links between geodiversity and biodiversity—and between geodiversity variables and other environmental variables. Predictive modelling and mechanistic exploration of geodiversity's contributions to species diversity were beyond the scope of this study.

Considering the novelty of geodiversity–biodiversity approach especially in the freshwater ecosystems, we wanted to find out whether the approach is feasible in the first place—and whether the same geodiversity variables used in terrestrial geodiversity–biodiversity research, such as georichness measures, could be applied to freshwater geodiversity–biodiversity research.

First, we generated generalised linear models (GLMs) to identify the important predictor variables from a selection of local, geodiversity and climate variables. We used automated model selection using the 'dredge' function from the 'MuMIn' package (Barton 2017) with AICc criteria in R (Burnham & Anderson 2004; R Development Core Team 2008). We were interested in how often (and which) geodiversity variables were included in the GLMs. We also used variation partitioning (Legendre & Legendre 2012) to assess the independent and shared contributions of these variable groups (local, geodiversity, climate) in explaining the variation in aquatic plant species richness (following Guisan & Zimmermann 2000 and Hawkins *et al.* 2003). Finally, we used boosted regression trees to estimate the relative influence of each environmental variable on each response variable (Elith *et al.* 2008) using the R package 'gbm' (Ridgeway *et al.* 2017) and function 'gbm.step' (Hastie *et al.* 2001). This was done to complement the automated GLM selection in order to identify single important variables in explaining aquatic plant species richness.

Correlative methods, such as simple correlation tests or GLMs, provide evidence of possible associations between variables, but do not imply causation. They are useful in contexts such as testing less studied or unknown relationships, including the relationship between geodiversity and biodiversity (or georichness and species richness). Consistent correlations can help in the design of further experiments. In Paper III, we used a Pearson correlation test to investigate the relationship between georichness datasets in Finland (geodiversity data validation) and georichness and vascular plant species richness in Finland and Switzerland (demonstration and validation of data use). All methods are described in more detail in the original research papers, Paper II and Paper III.

7 Results

In this chapter, I introduce the main results of each paper one-by-one. The summary of main findings and contributions of each paper is presented in Table 3. The main findings are discussed in the results section and the main contributions in the discussion section (Chapter 8).

Table 3. Thesis objectives, research questions, main findings and main contributions paper-by-paper.

	Paper I	**Paper II**	**Paper III**
Thesis objective	To provide theoretical and methodological premise to study landscape geodiversity in relation to biodiversity		
Paper objectives (O)	**O1** To review the current understanding and knowledge gaps of geodiversity–biodiversity research.	**O2** To empirically test the geodiversity–biodiversity relationship in freshwater ecosystems.	**O3** To provide tools for Europe-wide geodiversity–biodiversity research.
Research questions (RQ)	**RQ1** How does current empirical evidence support theoretical background of geodiversity–biodiversity relationship at landscape-scale? **RQ2** What are the methodological gaps in geodiversity assessment in biodiversity investigation?	**RQ3** How are geodiversity and biodiversity linked in freshwater ecosystems? **RQ4** Is grid-based geodiversity assessment suitable for biodiversity investigations in freshwater ecosystems?	**RQ5** How does the European geodiversity data contribute to quantitative geodiversity assessment? **RQ6** How can European geodiversity data be applied in biodiversity investigations?
Main findings	Geodiversity–biodiversity research is scattered, but parallel results from empirical research and strong theoretical background encourage more research. Major knowledge gaps concern conceptual and methodological inconsistency and bias in (empirical research related bias) scales, geographical areas and organismal groups.	We observed a positive link between catchment geodiversity and aquatic plant species richness, supporting the idea of geodiversity providing foundation for biodiversity that can extend and operate beyond ecosystem boundaries.	The provision of Europe-wide, versatile geodiversity data that establishes quantitative geodiversity assessment and enables continent-wide geodiversity and biodiversity research.
Main contributions	An introduction for geodiversity–biodiversity research and an overview of the empirical studies.	An empirical research example of applying grid-based geodiversity data in aquatic biodiversity context and an introduction of complementary catchment-scale approach for freshwater conservation.	A European geodiversity data for empirical geodiversity–biodiversity investigations and explicit guidelines for grid-based geodiversity assessment across large extents.

7.1 Current understanding and knowledge gaps of geodiversity–biodiversity research (Paper I)

In Paper I, we summarised the background and current understanding of the relationship between geodiversity and biodiversity in order to provide common guidelines for further geodiversity–biodiversity research.[3] First, we introduced the theoretical background on why geodiversity and biodiversity are related. We then reviewed previous empirical geodiversity–biodiversity studies and their perspectives, methodologies and results. We also examined the studies in terms of their spatial scale and discussed the relationship between geodiversity and biodiversity at local, landscape and continental scales with explicit research examples. Finally, we summarised guidelines for future research efforts and identified the most pressing knowledge gaps.

Considering the framing of this thesis, I will focus especially on the empirically observed landscape-scale relationship (RQ1), where the presumption is that geodiversity and biodiversity are positively related via high abiotic heterogeneity. In addition, I examine the methodological gaps that hinder systematic and effective geodiversity–biodiversity research (RQ2).

7.1.1 Research question 1

The first research question was: **How does current empirical evidence support theoretical background of geodiversity–biodiversity relationship at landscape-scale?** To review the empirical observations on the relationship between geodiversity and biodiversity, we categorised the research according to the scale of the study: local, landscape and continental. The majority of empirical studies focus on the landscape scale, examining single regions (such as a catchment area or a state) or countries, and primarily using terrestrial vegetation as the subject of study. Geodiversity has been found to contribute to vegetation diversity globally, including studies from Finland (Hjort *et al.* 2012; Räsänen *et al.* 2016; Tukiainen *et al.* 2017b), UK (Bailey *et al.* 2017, 2018), Australia (Keith 2011), China (Dakhil *et al.* 2021), USA (Nichols *et al.* 1998), Caribbean (Batlle & van der Hoek 2021) and Brazil (dos Santos *et al.* 2019). The consistent positive relationships observed, regardless of study area or assessment method, suggest that geodiversity variables should be more widely included in biodiversity studies. However, there is a need to expand empirical studies to include different taxa and ecosystems, as current evidence on the relationship between geodiversity and biodiversity is largely limited to terrestrial environments (see also Alahuhta *et al.* 2020).

Despite these simultaneous observations, separating or identifying the contribution of geodiversity to biodiversity can sometimes be challenging. Generalisations about their relationship often remain elusive because of the different focus of studies: some investigate multiple geodiversity variables, while others focus on individual components or processes. Furthermore, the relationship between geodiversity and biodiversity is not always straightforward; there are cases where climatic or local physical variables are found to be more influential on species than geodiversity factors, even though geodiversity variables add value to species diversity modelling (e.g. Bailey *et al.* 2017).

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[3] Our literature search was based on using 'geodiv*' AND 'biodiv*' as the 'topic' words in Web of Science search, yet search results were manually complemented due to variable and inconsistent use of the term 'geodiversity'. Same search approach was used and described in Alahuhta *et al.* (2020).

This is also likely to be the case in high-productivity systems where biotic ecosystem functions outweigh geodiversity contributions (cf. Wallis *et al.* 2022) or when the relationship between geodiversity and biodiversity changes along land use gradients (e.g. Ren *et al.* 2021; Tukiainen *et al.* 2017a). For instance, in a high-intensity land use region in western Finland, water chemistry and land use variables were found to be more important for stream biodiversity (including macroinvertebrates, diatoms and bacterial communities) than catchment-scale geodiversity variables (Kärnä *et al.* 2019). Nevertheless, geodiversity variables were still considered valuable complementary tools for freshwater conservation.

The review of empirical studies identified conceptual issues and gaps related to the definition of geodiversity. In structuring the review, we adopted Gray's (2013) definition of geodiversity, which is the most commonly used definition in the literature (Boothroyd & McHenry 2019). Specifically, we explored how various components—such as geology, soil, geomorphology, topography and hydrology—have been incorporated into geodiversity–biodiversity studies. While individual components of geodiversity, such as topography or soils, have been previously studied in relation to biodiversity, we emphasised the importance of a holistic view of the abiotic environment (see also Maliniemi *et al.* 2024). We chose to distinguish between topography and geomorphology because of the long tradition of using topographical variables in ecological and biogeographical research, but also to point out that topography is only one part of geodiversity.

To support future empirical research on the relationship between geodiversity and biodiversity, we recommend the establishment of clear frameworks and concepts, the systematisation of methodology, and the broadening of the research focus to include different scales, geographical areas and groups of organisms.

7.1.2 Research question 2

The second research question was: **What are the methodological gaps in geodiversity assessment in biodiversity investigations?** Methodological gaps in geodiversity assessment are closely related to conceptual gaps. The concept and definition of geodiversity is still evolving, which hinders the development of consistent approaches to qualify and quantify geodiversity. The generalisation of empirical evidence on the relationship between geodiversity and biodiversity is limited by the different approaches and measures of geodiversity; for example, geodiversity can be described as a single topographic variable or as a complex geodiversity index measure that takes into account the wide range of abiotic diversity. As a result, the wide range of different geodiversity indices are not fully comparable.

Empirical geodiversity–biodiversity studies predominantly use quantitative assessment methods, such as richness variables (e.g. Hjort *et al.* 2012) or other geodiversity indices (e.g. Najwer *et al.* 2016). Remote sensing and GIS data describing geological, pedological, geomorphological and hydrological features are frequently used to produce those indices (see also Boothroyd & McHenry 2019), but indicators implying energy or resource availability have also been used to describe geodiversity (e.g. NDVI in Wallis *et al.* 2022 or soil fertility in Dakhil *et al.* 2021). Variation in the environmental characteristics used to describe geodiversity diminishes the comparability between indices and results. Additionally, the wide range of geodiversity variables, from rock types to NDVI, can blur the concept of geodiversity (Maliniemi *et al.* 2024). However, the choice of environmental characteristics may also be influenced by regional data availability.

There is also a wide variation in the methods used to assess geodiversity, depending on the scale of the study. Qualitative methods are typically used at local scales and for geoconservation objectives (e.g. geosite assessment), while quantitative methods are more often used at larger spatial resolutions and extents. In continental and landscape-scale studies, where the aim is usually to identify broad-scale diversity patterns and links between geodiversity and biodiversity, grid-based methods are often used, although alternative methods for delineating landscape units have been presented, particularly for conservation applications (e.g. Albano *et al.* 2015). Plot-scale studies can elucidate the underlying mechanisms of observed geodiversity–biodiversity connections, for instance by observing soil properties and functions (e.g. De Falco *et al.* 2021). Yet, common methodological guidelines for quantitative local-scale assessments of geodiversity in ecological contexts are even scarcer than at the landscape scale (but see Crisp *et al.* 2023; Hjort *et al.* 2022).

Most geodiversity assessments still focus solely on geodiversity assessment (either qualitatively or quantitatively), where the discussions of the link between geodiversity and biodiversity may remain theoretical rather than being empirically tested, if present at all (see also review by Crisp *et al.* 2021). It is therefore unclear to what extent these assessement methods are appropriate for biodiversity studies. Furthermore, in some qualitative or discursive study settings, geodiversity may only be used to frame the study or to refer generally to all non-living diversity.

7.2 Empirical observations from Finnish lakes and rivers (Paper II)

In Paper II, we examined the relationship between geodiversity and biodiversity in freshwater ecosystems. We were interested in whether the positive relationship observed in terrestrial systems could also be observed in less studied freshwater systems. As we also wanted to test the existing Finnish geodiversity dataset describing terrestrial geodiversity in Finland, geodiversity was assessed from the catchment areas of the water bodies. Freshwater biodiversity was measured as aquatic plant species richness.

7.2.1 Research question 3

The third research question was: **How are geodiversity and biodiversity linked in freshwater ecosystems?** We found out that catchment geodiversity was positively correlated with aquatic plant species richness (Table 4). The observed patterns were similar in two different habitats (lakes and rivers) and two different functional plant groups (helophytes and hydrophytes). Geodiversity variables were examined in relation to the more commonly used environmental variables, of which the local scale variables (e.g. alkalinity, lake area, river width) explained most of the variation in aquatic plant species richness. However, geodiversity contributed to the variation despite of the habitat type or the functional group, highlighting the importance of the catchment area materials and processes for a water body (see Figure 5 in Paper II for variation partitioning between local, geodiversity and climate variables, Toivanen *et al.* 2019).

While the overall evidence for the positive contribution of geodiversity was consistent, there were also differences between habitats. The relationship between catchment soil, rock and geomorphological variables and species richness was positive in both habitats, but the correlations were consistently lower in rivers (Table 4). Also, the variation explained by GLMs was greater in lakes (adj. D^2=0.41–0.43) than in rivers (adj. D^2=0.18–0.21) (see also Table 1 in Paper II, Toivanen *et al.* 2019). This is likely due to the focus on only one group of organisms, as lentic and lotic environments are very different types of environments for aquatic species. In general, aquatic plants (especially hydrophytes in our data) are not as abundant in running waters as in lentic lake environments. Thus, other groups of organisms such as macroinvertebrates, bacteria or diatoms would probably provide a complementary perspective (see e.g. Kärnä *et al.* 2019).

Of the individual geodiversity variables, soil variation showed the strongest correlations (Table 4) and relative influence (see Figure 6 in Paper II, Toivanen *et al.* 2019) especially for helophyte richness, which may reflect the stronger response of helophytes to eutrophication and land use (see e.g. Alahuhta *et al.* 2016; Kolada 2016). Geomorphological variation, on the other hand, was the most important variable for hydrophytes, although there were not as clear differences in the relevance of geodiversity variables within hydrophytes as within helophytes. However, if the geomorphological heterogeneity at the catchment scale also reflects the geomorphological heterogeneity within a river reach (or lake), the variety of geomorphological features may create more diverse habitats, with both lower and higher flow rates supporting different functional groups of aquatic plants—and thus promoting hydrophyte richness.

Table 4. Spearman correlations between catchment geodiversity variables (std=standard deviation) and species richness variables in lakes (n=145) and rivers (n=146). ns=no statistical significance.

	Soil richness (std)	**Rock richness (std)**	**Geomorphological richness (std)**
Lakes (all taxa)	0.42 (p<0.001)	0.32 (p<0.01)	0.35 (p<0.001)
Helophytes	0.55 (p<0.001)	0.27 (p<0.01)	0.16 (ns)
Hydrophytes	0.13 (ns)	0.24 (p<0.01)	0.39 (p<0.001)
Rivers (all taxa)	0.31 (p<0.01)	0.14 (ns)	0.34 (p<0.001)
Helophytes	0.36 (p<0.001)	0.11 (ns)	0.27 (p<0.01)
Hydrophytes	0.13 (ns)	0.13 (ns)	0.35 (p<0.001)

7.2.2 Research question 4

The fourth research question was: **Is grid-based geodiversity assessment suitable for biodiversity investigations in freshwater ecosystems?** The results of the study demonstrated that grid-based geodiversity assessment method is particularly suitable for catchment-scale studies because it allows the simultaneous inclusion of a wide variety of abiotic characteristics of the catchment. Catchment geodiversity can simultaneously describe the geological, pedological and geomorphological heterogeneity of the catchment area.

The observed positive relationship between geodiversity and biodiversity is also a reminder that water bodies are not 'islands' or separate entities surrounded by the terrestrial realm, but rather interconnected entities influenced by various fluxes and processes, underlining their interdependence. This perspective is in line with the Conserving Nature's Stage concept, which suggests that protecting the abiotic environment can benefit both freshwater and terrestrial biodiversity within catchment areas. Additionally, the observed positive link encourages further exploration of the geodiversity–biodiversity relationship employing the grid-based assessment methods that extend across ecosystems. Species and communities are affected by environmental factors across various scales, and geodiversity can serve as a landscape-scale environmental variable in these contexts.

As an additional investigation, we explored the feasibility of applying the grid-based assessment at a more local scale (see Appendix 4 in Paper II, Toivanen *et al.* 2019). To investigate this, we assessed geodiversity within a 1-km shoreline buffer zone and correlated these shoreline geodiversity variables (standard deviation of soil, rock and geomorphological richness) with catchment area geodiversity variables (standard deviation of soil, rock and geomorphological richness) and species richness variables (all taxa, helophyte and hydrophyte richness). The geodiversity variables from shoreline and catchment areas showed a strong positive correlation with each other (r_s=0.64–0.77, $p<0.001$). Similarly, species richness variables correlated positively with shoreline geodiversity variables, and they were very similar to correlations between species richness and catchment geodiversity variables (see Table S4.9 in Paper II, Toivanen *et al.* 2019). However, this analysis was limited to lakes, as it was not meaningful to apply a similar buffer zone approach to rivers (using point feature data). Nonetheless, this additional investigation suggests that both catchment and shoreline geodiversity assessment methods should be further developed and investigated in relation to aquatic biodiversity.

7.3 European geodiversity to support future broad-scale research (Paper III)

In Paper III, we provided a Europe-wide geodiversity data for further geodiversity–biodiversity investigations (Figure 8). Based on the literature and our own empirical studies, grid-based geodiversity assessments are suitable for various large-scale geodiversity and biodiversity investigations (cf. Tukiainen *et al.* 2017a, 2017b; Tukiainen & Hjort 2019). Therefore, we have applied this method to produce continental-scale geodiversity data for applied use. The data are deposited in the Dryad repository (Toivanen *et al.* 2024b).

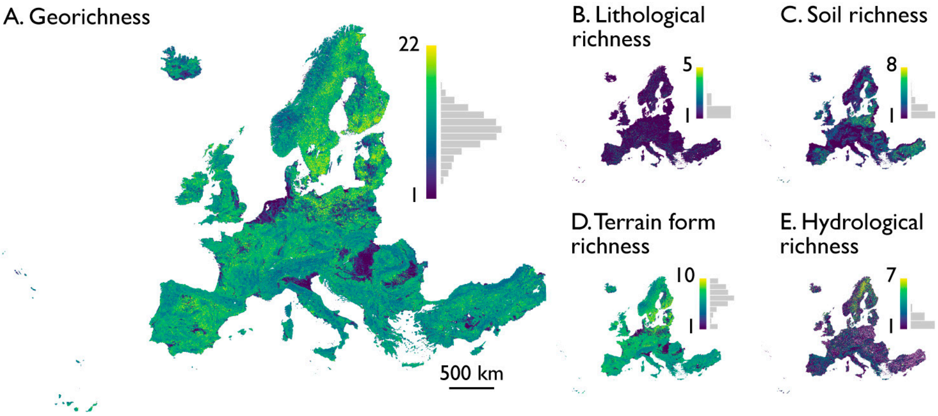

Figure 8. Georichness at 1-km resolution across Europe, based on Paper III (Toivanen *et al.* 2024a). Georichness is a sum of lithological richness (B), soil richness (C), terrain form richness (D) and hydrological richness (E). Similar data was produced at 10-km resolution and those figures can be found in Paper III.

7.3.1 Research question 5

The fifth research question was: **How does the European geodiversity data contribute to quantitative geodiversity assessment?** In Paper III, we compiled a comprehensive geodiversity dataset describing terrestrial geological, pedological, geomorphological and hydrological diversity (Figure 8B–E). We evaluated the data with the Finnish geodiversity dataset (Tukiainen *et al.* 2017a, 2017b) using correlation analysis. Both datasets extensively describe the diversity of abiotic nature across landscapes, despite the differences between the geodiversity components and individual geofeatures (described in more detail in Chapter 6 and Paper III). Even though the source data were independent of each other, the European and the Finnish georichness variables showed positive correlations (r_p=0.37, p<0.001 at 1-km and r_p=0.59, p<0.001 at 10-km resolution).

While the European geodiversity dataset is primarily produced for applied biodiversity studies, it offers opportunities to advance quantitative geodiversity, which can help both to better understand geodiversity itself and to study the relationship between geodiversity and biodiversity from different perspectives (e.g. alpha, beta and gamma geodiversity in Tukiainen *et al.* 2023). In Paper III, we used a simple richness index to describe geodiversity. By adopting some other (e.g. ecologically inspired) quantitative assessment methods, it is possible to further develop the quantitative assessment, as we also provide areal coverage details for each geofeature. Additional inspiration for the further development of quantitative geodiversity assessment can be found in pedological research, where various diversity indices have been used more regularly (e.g. Ibáñez *et al.* 1995; McBratney & Minasny 2007).

The grid-based quantitative approach here also suggests an alternative approach to previous assessments of continental geodiversity, as seen by Wolniewicz (2023), who focused specifically on the use of continental geodiversity in geoconservation and geoheritage assessment, in contrast to the biodiversity-related motives in our work.

7.3.2 Research question 6

The sixth research question was: **How can European geodiversity data be applied in biodiversity investigations?** We evaluated the suitability of the geodiversity dataset for biodiversity studies by correlating geodiversity variables with vascular plant species richness in two different study areas: Finland and Switzerland. In both countries we observed statistically significant positive correlations between georichness and species richness at 10-km resolution (Finland r_p=0.34, p<0.001, Switzerland r_p=0.26, p<0.001). The correlative demonstration of the dataset suggests that European geodiversity data can be useful for further biodiversity investigations, and the results are consistent with previous studies suggesting a positive relationship between geodiversity and plant richness (e.g. Bailey *et al.* 2017; Batlle & van der Hoek 2021; Hjort *et al.* 2012).

We provide the geodiversity dataset at two spatial resolutions, 1-km and 10-km. In addition to the georichness variables used in the geodiversity–biodiversity demonstration, the data also include more specific information on the presence of individual geofeatures per 1-km and 10-km grid cell, as well as the areal coverage of each geofeature per grid cell. Thus, there are both ready-to-use variables (georichness, geological richness, pedological richness, terrain form richness, hydrological richness) and more detailed information about individual geofeatures that enable producing other diversity measures of geodiversity, such as assessing how the 'communities' of geofeatures contribute to total geodiversity (cf. species communities) (see also Alahuhta *et al.* 2024 on geodiversity uniqueness).

We encourage the use of data in geodiversity–biodiversity studies at different resolutions, in different ecosystems and with different groups of organisms, to gain a broader understanding of the relationship between geodiversity and biodiversity. Macroecology often relies on climate data and how climate creates or controls biodiversity gradients (see e.g. Heino *et al.* 2015), although climatic variables may not be the best predictors of diversity at the ecosystem level (cf. Simensen *et al.* 2020). Geodiversity, on the other hand, can provide insight to more regional properties or processes (cf. Gerstner *et al.* 2024) or better reflect biodiversity and its changes over time (cf. Simensen *et al.* 2020).

While the European geodiversity data are suitable for Europe-wide exploration, they can also be used in more regional research settings with more specific regional knowledge of both biodiversity and geodiversity of the region. With more specific regional knowledge, the data can be edited or supplemented with more precise taxonomic or spatial information. Overall, both empirical and methodological developments are encouraged.

8 Discussion

The main aim of this thesis is to provide theoretical and methodological premise to study landscape-scale geodiversity in relation to biodiversity. This was done by first reviewing the status of geodiversity in biodiversity investigations, and then providing empirical evidence and methodological tools for further research endeavours.

This thesis contributes to geodiversity research from multiple perspectives. In Paper I, I establish and develop the common understanding and guidelines for further geodiversity–biodiversity research (**O1**). In Paper II, I provide an empirical research example of applying grid-based geodiversity data in aquatic biodiversity context, that also has implications to catchment-scale nature conservation and planning (**O2**). In Paper III, I further establish the grid-based geodiversity assessment with a ready-to-use geodiversity dataset that enables Europe-wide geodiversity–biodiversity investigations (**O3**).

The combination of a literature review (Paper I), an empirical research paper (Paper II) and data products (Paper III) in this thesis provides a set of guidelines for grid-based geodiversity assessment at landscape-scale for biodiversity investigations. It also serves as a source of inspiration for diverse geodiversity research and promotion, facilitating a deeper understanding of geodiversity and its integration into practical actions, such as nature conservation, and discussions on various environmental topics and issues.

In the discussion section, I begin by addressing conceptual knowledge gaps (Chapter 8.1), and how to consider them in future empirical studies (Chapter 8.2). Then, I explore the journey toward methodologically systematic and conscious research (Chapter 8.3), highlighting the complementary nature of various assessment approaches (Chapter 8.4). Following this, I discuss the reasoning and strategies for integrating geodiversity into nature conservation efforts (Chapter 8.5). Finally, I examine both the potential and limitations of geodiversity in biodiversity investigations (Chapter 8.6) and suggest themes for future research within the scope of this thesis (Chapter 8.7).

8.1 Conceptual hurdles in including geodiversity in biodiversity investigations

Geodiversity–biodiversity research is very scattered, despite its increasing numbers. While there is growing interest in integrating geodiversity into biodiversity research, our observations in Paper I suggest that the complexity of the geodiversity concept poses challenges in its application (see also reviews by Boothroyd & McHenry 2019 and Crisp *et al.* 2022). Although the theoretical interest in geodiversity–biodiversity studies is well-reasoned, several conceptual, empirical and methodological gaps hinder scientific and applied advancements in this field (see also Maliniemi *et al.* 2024; Schrodt *et al.* 2024). There is therefore a need to establish common guidelines for future research to improve understanding of how geodiversity contributes to biodiversity.

Previous reviews and perspective papers have promoted different aspects of geodiversity, including developing and strengthening the concept of geodiversity (e.g. Gray 2008b, 2021; Hjort *et al.* 2024; Ibáñez & Brevik 2022; Serrano & Ruiz-Flaño 2007), promoting geoheritage and geoconservation (e.g. Crofts *et al.* 2020; Ibáñez *et al.* 2019), recognising geodiversity in a wider conservation context (e.g. Gordon & Barron 2012; Gordon *et al.* 2022; Knudson *et al.* 2018), reviewing geodiversity assessment methods (e.g. Zwolinski *et al.* 2018; Crisp *et al.* 2021), integrating geodiversity into sustainable resource management and environmental monitoring (e.g. Brilha *et al.* 2018; Schrodt *et al.* 2019, 2024), linking eco- and geosystem services (e.g. Anougram *et al.* 2024; Fox *et al.* 2020; van Ree *et al.* 2017), and introducing new avenues of research, such as how geodiversity can promote human health (Alahuhta *et al.* 2023).

While these perspectives often draw parallels between geodiversity and biodiversity, few reviews have explicitly focused on their relationship. Although Boothroyd & McHenry (2019) and Crisp *et al.* (2022) have evaluated the inclusion of geodiversity in biological discourse and biodiversity assessment, their focus was on providing quantitative insights of previously published geodiversity–biodiversity papers. To complement these reviews, our aim in Paper I was to provide theoretical and conceptual background for future geodiversity–biodiversity investigations (**O1**, Table 3).

Based on our observations in Paper I, empirical geodiversity–biodiversity research sometimes employs geodiversity vaguely, without clear definitions or links to specific environmental variables (see also Maliniemi *et al.* 2024), although researchers generally agree on Gray's (2013) definition of geodiversity (Boothroyd & MacHenry 2019). This ambiguity, coupled with the diverse assessment methods (cf. Crisp 2021, 2022), limits the ability to draw generalised conclusions from geodiversity–biodiversity research, despite evidence of a positive relationship between the two.

To overcome the vague use of geodiversity, in Paper I, we presented an overview of the scales used (i.e. local, landscape, global) and the inclusion of different geodiversity components (i.e. geology, soil, hydrology, geomorphology, topography) in previous geodiversity–biodiversity studies. Most of these studies describe a clear framework for understanding geodiversity, including methods of assessment and rationale for variable selection. However, we particularly emphasise the importance of considering multiple components simultaneously to capture a broader range of abiotic variation in empirical geodiversity–biodiversity studies (see also Crisp *et al.* 2022). Furthermore, as geodiversity becomes more mainstream, continued interdisciplinary dialogue between geoscientists and bioscientists remains essential to establish a shared understanding of geodiversity and its implications for biodiversity (see also Boothroyd & MacHenry 2019).

A common argument against geodiversity in ecological discourse is that geodiversity is just 'environmental heterogeneity', which is already commonly used in ecological research, making geodiversity redundant (see also Maliniemi *et al.* 2024). However, environmental heterogeneity variables often overlook the comprehensive diversity encompassed by geodiversity and fail to recognise the intrinsic value of geodiversity. When attitudes towards geodiversity are favourable, the term can still be used arbitrarily. For example, a single variable of topographic heterogeneity is sometimes used as a proxy for all geodiversity. While it can capture a lot of abiotic variation in a single variable and act as a powerful proxy variable for geodiversity, more research is needed on how such variables relate to other geodiversity components (see also discussion in Schrodt *et al.* 2024).

Although researchers, especially geo(eco)logists, have long discussed the inherent connection between geodiversity and biodiversity (e.g. Santucci 2005 on the emergence of the term 'geodiversity'), conceptual frameworks for integrating geodiversity into biodiversity research are only beginning to emerge (see e.g. Hjort *et al.* 2022; Lausch *et al.* 2024; Vernham *et al.* 2023; Zarnetske *et al.* 2019). Strong conceptual frameworks, such as a universal geodiversity taxonomy (cf. Hjort *et al.* 2024) or systems for quantifying geodiversity (cf. Crisp *et al.* 2022; Zwolinski *et al.* 2018), can help overcome the conceptual hurdles. They also facilitate the application of geodiversity in biodiversity research across spatial and temporal scales, from local to global assessments. The contributions of geodiversity vary across scales, from the creation of microhabitats at the local scale to the shaping of geological patterns at the continental scale (Figure 4 in Paper I; see also Lawler *et al.* 2015). There is therefore a further need to define what components of geodiversity mean at different scales, particularly in the context of supporting biodiversity (see also Tukiainen, Bailey & Hjort, manuscript). Studies at local scale can shed light on the mechanisms underlying the relationship between geodiversity and biodiversity, while studies at landscape to global scale can provide valuable insights into the coarse-filter conservation actions.

8.2 From conceptual understanding to empirical applications

To gradually move from conceptual gaps to practical solutions, and to better demonstrate how geodiversity variables can be constructed and incorporated in practice, we need to examine geodiversity components beyond just geological, pedological, geomorphological and hydrological diversity. In line with the main objective of this thesis to establish a theoretical and methodological foundation for studying geodiversity (Table 3), I introduce few alternative perspectives for observing geodiversity in Chapter 2. While I extensively describe all geodiversity components, from their physical features to chemical characteristics, I also offer a more structured premise as compositional, structural and functional perspectives (Table 1). These perspectives parallel with the compositional, structural and functional measures employed in biodiversity studies (see e.g. Noss 1990).

Compositional diversity is in the centre of this thesis, as I focus on assessing geodiversity as the presence and absence of distinct 'geofeatures' (cf. species), which are summed into a 'georichness' variable (cf. species richness) within study grids. Additionally, I assessed catchment area geodiversity as the variation of abiotic features across the catchment, representing the heterogeneity of the abiotic environment within these catchments (cf. structural diversity). If included, functional geodiversity would assess the properties and processes that contribute to biodiversity within the catchment.

Given the proposed positive link between geodiversity and biodiversity, geodiversity has potential as a proxy for biodiversity, although its effectiveness is likely to be context dependent. In Paper II, we aimed to contribute to this discourse by examining the relationship between geodiversity and biodiversity in freshwater ecosystems (**O2**, Table 3). While we observed a positive relationship between catchment geodiversity and aquatic plant species richness, further empirical investigations are needed to assess the consistency of this relationship across different regions, taxa and environmental conditions (but see Kärnä *et al.* 2019). Investigations could include examining the relationship between geodiversity and biodiversity along land use gradients, across different groups of organisms in different ecosystems, and taking into account variations in the size of lakes, rivers or their catchments. In addition to the compositional and structural perspectives of geodiversity derived from georichness variables, incorporating measures of functional diversity (such as factors related to river flow dynamics) into assessments of geodiversity is likely to provide valuable insights into the range of geo- and ecosystem functions that underpin biodiversity within water bodies and their surrounding catchments.

However, our findings in Paper II highlight the interconnectedness of aquatic and terrestrial ecosystems (see also Heino *et al.* 2020; Soininen *et al.* 2015). Consideration of catchment characteristics and activities is crucial for assessing the status of freshwaters and their biodiversity (rivers in Heino *et al.* 2022; lakes in Heino *et al.* 2023). In Finland, a roadmap for catchment planning was devised in 2024 to align with EU-led goals for the good status of both above- and below-ground waters by 2030 (Rytkönen *et al.* 2024). While not explicitly stated in the roadmap document, geodiversity is inherently linked to the proposed actions. It is essential to consider geological, pedological, geomorphological and hydrological features and processes across catchments when implementing key actions to support catchment planning, such as wetland, peatland and riverbed restoration. The restoration of these ecosystems not only affects water quality and the biodiversity of aquatic ecosystems by regulating water flow and controlling the runoff of sediment and nutrients, but it also enhances the diversity of habitats across the entire catchment area. Therefore, integrating geodiversity into catchment planning facilitates the implementation of nature-based solutions that can effectively manage water resources, enhance biodiversity, and support various ecosystem and geosystem functions.

In general, geodiversity has the potential to be a multidisciplinary concept, building bridges between geographers, geoscientists and bioscientists, as well as aquatic and terrestrial ecologists. Often researchers focus on their own area of expertise and overlook the interactions between different environments. Given the increasing interest in large-scale studies testing the positive geodiversity–biodiversity hypothesis, future research would benefit from improved geodiversity frameworks to ensure comparable assessments. In addition, readily available geodiversity data accessible across disciplines would facilitate research efforts.

In Finland, for example, a national geodiversity data has been extensively studied in a number of contexts. These include regional geodiversity patterns (Tukiainen & Hjort 2021), the contribution of geodiversity to ecosystem services (Alahuhta *et al.* 2018), and geodiversity patterns along land use gradients (Tukiainen *et al.* 2017a). Furthermore, investigations on geodiversity–biodiversity relationship have been conducted in both terrestrial (Räsänen *et al.* 2016; Tukiainen *et al.* 2017b) and aquatic (Kärnä *et al.* 2019; Toivanen *et al.* 2019) environments. It is reasonable to assume that the availability of geodiversity data would facilitate a greater number of investigations, allowing more robust generalisations to be made about the contributions of geodiversity and its potential applications. In addition, future research efforts would benefit from collaboration across disciplinary boundaries, given the broad potential for the use of geodiversity data.

8.3 Towards methodologically systematic and conceptually conscious geodiversity research

The review presented in Paper I and the empirical exploration presented in Paper II both indicated that the grid-based geodiversity assessment technique has significant potential for use in biodiversity investigations (see also Crisp *et al.* 2021). Therefore, in Paper III, our objective was to provide further support for the establishment of grid-based assessment methods and to offer a readily usable geodiversity data set for biodiversity investigations (**O3**, Table 3). Given the previous, somewhat vague use of geodiversity in empirical explorations, the introduced European geodiversity data provides a valuable resource for researchers seeking to incorporate geodiversity variables in their studies.

While it is important to study each component of geodiversity individually, studies that concentrate on geo*diversity* as a whole remain relatively limited in number. For example, topography is often used as a generic proxy for geodiversity, particularly at broad scales, due to the lack of comprehensive and harmonised geomorphological datasets. A variety of topographic variables, including landforms and wetness indices, can be calculated from globally available remote sensing (RS) and geographic information system (GIS) data (e.g. Amatulli *et al.* 2020; Sørensen *et al.* 2006). Geological and pedological data may also be available, but are often limited to specific regions or countries. Although various data on abiotic nature are available, harmonised, spatially and temporally comprehensive data are still lacking for almost all parts of geodiversity (see also Schrodt *et al.* 2024).

In the construction of the European geodiversity data set (Paper III), we employed open-access, harmonised geological, pedological, geomorphological and hydrological datasets. Drawing from the experience gained from the Finnish geodiversity dataset, the European data were calculated using similar zonal analysis methods. In specific, we demonstrate the use of 'georichness' variable. Used as such, georichness variables offer a comprehensive measure of geodiversity to be used in the analysis. However, it is also possible to select a subset of geodiversity components (lithology, soils, terrain forms, hydrological features) that are relevant to the specific study context. Investigating these components separately provides insight into their individual contributions to biodiversity.

We focused especially on georichness, because we believe that introducing concurrent assessment methods of both biodiversity and geodiversity reinforce the status of geodiversity as an integral component of natural diversity alongside biodiversity. In addition, georichness is relatively easy to calculate based on available GIS data, and it has proven useful in previous empirical geodiversity–biodiversity studies at the landscape scale (see Paper I and further support in the findings of Paper II). Therefore, this approach facilitates smoother comparisons and study settings for investigating the relationship between geodiversity and biodiversity, building upon previous knowledge of spatial biodiversity patterns.

To extend the conceptual framework and acknowledge that the grid-based assessment method is not confined to richness measures, Paper III provides comprehensive information on individual geofeatures, including their areal coverage within each 1-km and 10-km grid cell. This level of detail enables researchers to selectively include specific geofeatures or calculate various diversity measures beyond richness variables (geofeature areal coverage used e.g. in Bailey *et al.* 2017). Furthermore, in biodiversity research, the concepts of alpha, beta and gamma diversity are commonly employed to examine biodiversity from complementary perspectives. These concepts can also be applied to geodiversity (Tukiainen *et al.* 2023).

In Paper III, we provided a brief demonstration of the data application in geodiversity–biodiversity investigations, specifically by correlating vascular plant species richness and georichness in Finland and Switzerland. This was done to demonstrate the potential of the data to be used use in different ecosystems and at various spatial scales, ranging from continental, regional and ecosystem-wide applications. Ideally, these data and explicit guidelines for grid-based geodiversity assessment across large extents will stimulate further empirical studies on the geodiversity–biodiversity relationship. This should include investigations in various environments and spatial scales, as well as studies with regional expertise and data from different ecosystems and organismal groups.

8.4 Different assessment approaches complement each other

The quantitative assessment of geodiversity plays a crucial role in understanding the spatial heterogeneity of abiotic features in landscapes, as well as their ecological significance. It can provide valuable information for land management, environmental impact assessment and conservation efforts. While the European geodiversity data introduced in Paper III represents a significant advancement in continental geodiversity assessments, similar initiatives have recently emerged at both continental (Europe, Wolniewicz 2023) and global scales (Polman *et al.* 2024).

However, the still limited availability of large-scale geodiversity assessments highlights the need for alternative methodologies to complement existing datasets and address different research needs. For example, the assessments by Wolniewicz (2023) and Polman *et al.* (2024) are rooted in geoheritage and geoconservation, and aim to assess current conservation status and guide future conservation efforts, in contrast to the biodiversity-focused investigations in Paper III. Moreover, while Wolniewicz (2023) provides comprehensive European geodiversity maps, they do not offer data products for further use.

In their global geodiversity assessment, Polman *et al.* (2024) used a zonal analysis approach (similar to that used in our European geodiversity data) to investigate the inclusion of geodiversity components within UNESCO Global Geoparks. Instead of georichness, they produced a classified geodiversity score (from very low to very high, 1–5) at 10-km resolution. Their geodiversity index comprised of lithological diversity, soil diversity, topographical diversity and hydrological diversity, of which the soil diversity is based on the SoilGrids dataset (Hengl *et al.* 2017) also used in Paper III. Lithological and hydrological components were similar to our European data in Paper III, but the continental scale in our study allowed the use of more detailed source data. For instance, lithology had more detailed classification with almost double number of classes (GLiM vs. IHME1500 in Hartmann & Moosdorf 2012 and Duscher *et al.* 2015, respectively). More notably, Polman *et al.* (2024) described hydrological diversity as lake area and river length (based on HydroSHEDS in Lehner *et al.* 2011), while our European dataset included different wetland types (from Corine Land Cover) and groundwater features (from IHME1500) in addition to lakes and rivers.

These variations in source data highlight the different ways in which geodiversity can be characterised. Variables such as slope range, lake area or river length are not suitable for simple richness calculations, but provide complementary perspectives for understanding geodiversity (see also the mixed approach of grid-based richness and area variables in Bailey *et al.* 2017).

Wolniewicz (2023) employed an alternative assessment method to evaluate European geodiversity, with the aim of identifying geodiversity patterns and hotspots across the continent. More specifically, Wolniewicz (2023) used a centroid analysis and kernel density methods, which are applicable to natural resource management and land use planning (da Silva *et al.* 2019; Forte *et al.* 2018). Unlike the grid-based zonal analysis in Paper III and Polman *et al.* (2024), it is not fixed to any specific grid resolution, but is adjusted based on geofeatures and their spatial dynamics in the source data. As the source data for geodiversity, Wolniewicz (2023) used previously introduced data sources, such as GLiM (Hartmann & Moosdorf 2012) and SoilGrids (Hengl *et al.* 2017), terrain forms (Jasiewicz & Stepinski 2013), but also DEM-derived terrain ruggedness index (Riley *et al.* 1999) and complementary data to describe hydrological diversity as number of water bodies (Yamazaki *et al.* 2015) and hydrogeological diversity as groundwater table depth (Fan *et al.* 2015). In addition, GLiM was complemented with global unconsolidated sediments (Börker *et al.* 2018) to better capture the variety in lithological diversity.

The consistent use of similar source data in these independent assessments, from continental to global scale, suggests that there is agreement among researchers on how to comprehensively assess geodiversity and which of the existing data are most feasible to use in large-scale geodiversity assessments. While available data can still drive the assessment to some extent, the prevailing view is that different aspects of geology, pedology, geomorphology and hydrology should be considered.

At the global level, assessments still rely on modelled datasets such as GLiM (for lithology) or SoilGrids (for pedology), or widely available topographic indices to describe geomorphological variation in general. Hydrological diversity, by comparison, is still lagging behind in terms of availability. While the presence of lakes and rivers covers part of the hydrological diversity, it still disregards the complexity of aquatic features (e.g. springs, frozen water, or wetlands) and groundwater features (see also Hjort *et al.* 2024). Also, Alsbach *et al.* (2024) also discuss several alternative approaches to assessing hydrological diversity, including physical, chemical and functional features of rivers, in their study of the geodiversity of the Amazon basin, where they applied the global data of Polman *et al.* (2024).

While these research examples focused on assessing geodiversity at continuous and large scales, there are other large-scale examples of empirical geodiversity–biodiversity studies. For instance, Muellner-Riehl *et al.* (2019) studied global geodiversity–biodiversity relationship in mountain environments with a geodiversity data that corresponds to Polman *et al.* (2024), demonstrating the use of the same geodiversity data in different research context. In their geodiversity–biodiversity investigations, Read *et al.* (2020) described continental geodiversity in the United States with geological age, soil and elevation diversity variables, but also included a gross primary productivity (GPP) variable to account for resource availability. Considering such habitat variables as geodiversity variables is not unseen (see e.g. Wallis *et al.* 2022; Zarnetske 2019), yet using variables such as GPP or normalised vegetation index (NDVI) to describe geodiversity variables makes it hard to distinguish the contribution of geodiversity *per se*. Such variables have previously been used as proxies for biodiversity (e.g. Benedetti *et al.* 2023), thus using them as geodiversity proxies can cause confusion (see also Maliniemi *et al.* 2024).

In addition to continental-to-global scale investigations of the geodiversity–biodiversity relationship, a wide range of quantitative geodiversity assessment studies exist, even at very local scales (as discussed in Paper I). Some of these studies emphasise biodiversity and its conservation implications (e.g. de Paula Silva *et al.* 2021; Pereira *et al.* 2013; Santos *et al.* 2017), while others focus on a natural heritage perspective (e.g. Reynard & Coratza 2007 on geomorphosites), in which ecological values can also be integrated (e.g. Bollati *et al.* 2014 on ecological attributes of geomorphosites). Recognising and accepting that there are different purposes and perspectives for studying geodiversity helps to streamline quantitative assessments. Recent contributions from reviews of geodiversity assessments (e.g. Crisp *et al.* 2021; Zwolinski *et al.* 2018) also help to guide and establish the methodological developments and give room to appreciate their complementary nature.

8.5 Geodiversity in nature conservation

Conservation, whether approached from a biocentric or geocentric perspective, is at the centre of many geodiversity–biodiversity studies. While both perspectives are essential, their combined consideration may yield the most effective results. Conservation strategies aimed at preserving unique and rare biodiversity and geodiversity are crucial (see also Tukiainen & Bailey 2023). However, if we assume that both high biodiversity and high geodiversity are essential to support a wider range of geosystem and ecosystem functions, then equal emphasis should be placed on conserving both types of diversity. Efforts such as the global 30x30 conservation target (IUCN 2023) could benefit from recognising the potential overlap between geodiversity and biodiversity. However, further research is needed to elucidate the relationship between geodiversity and biodiversity across regions, taxa and ecosystems in order to target conservation efforts accordingly.

Many geodiversity–biodiversity studies are motivated by the Conserving Nature's Stage (CNS) conservation strategy in particular (e.g. Read *et al.* 2020; Ren *et al.* 2021; Tukiainen *et al.* 2017b), but few have tested its effectiveness in practice (see Miller *et al.* 2024). The CNS is based on the assumption that a heterogeneous environment provides a more diverse habitat for species, and that geodiversity can sustain biodiversity over longer timescales (Lawler *et al.* 2015). For instance, Paper II examined how a more heterogeneous catchment may support a more diverse aquatic life. However, it did not address the temporal aspect of CNS. While empirical studies on the temporal aspect of CNS would be valuable to truly assess how well geodiversity can sustain biodiversity over longer time scales, they are hampered by the lack of temporal species data. Furthermore, although geodiversity is seen as a stable foundation in the CNS strategy, it is also important to recognise the dynamic nature of some elements of geodiversity (e.g. geomorphological or hydrological processes) and the fact that geodiversity is also vulnerable to human activities and climate change (see e.g. Prosser *et al.* 2010; van Ree *et al.* 2024).

The interconnectedness of ecosystems and the abiotic and biotic nature are increasingly recognised in the context of global biodiversity frameworks and targets beyond 2020, such as 30x30. This is likely because conserving such large areas requires region-based analysis and consideration of whole ecosystems and landscapes. For example, the IUCN function-based ecosystem typology for conservation successfully draws attention to the abiotic environments and the importance of landscapes and seascapes (Keith *et al.* 2022). However, its planning is still based on biocentric diversity and ecosystem metrics (see also Comer *et al.* 2015). To put it bluntly, conservation efforts are targeted at the actors (i.e. biodiversity), rather than ensuring a functioning stage (i.e. geodiversity), even though the actions are likely to affect abiotic diversity as well (see also Zhu *et al.* 2022). However, IUCN has been promoting geodiversity in conservation efforts since 2009 (Dudley 2008) and has published specific guidelines for geoconservation in protected and conserved areas (Crofts *et al.* 2020).

A more active recognition of geodiversity has both scientific and practical benefits. In particular, at the landscape or ecosystem scale, conservation efforts could systematically use geodiversity to identify abiotic regimes or priority areas for protection and restoration, or to improve habitat connectivity and buffer zones to facilitate ecosystem resilience (cf. land facets in Brost & Beir 2012). This idea is also supported by growing evidence on geodiversity improving species richness models (e.g. Bailey *et al.* 2017; Miller *et al.* 2024). Simensen *et al.* (2020) also found that geodiversity-related variables improved 'ecosystem-level distribution modelling'. Thus, geodiversity could be used as an environmental surrogate, where geodiversity and climate are used in conservation planning when species data are not available (Beier *et al.* 2015). A similar idea is advocated in holistic diversity assessments, such as the EcoSyst framework (Halvorsen *et al.* 2020), which highlights the importance of including all biodiversity, geodiversity and climate when assessing diversity in ecosystems and landscapes. However, the lack of systematic, universal standardisation for abiotic diversity remains a challenge.

8.6 Potential and limitations of geodiversity in biodiversity investigations

The theory and growing empirical evidence demonstrate the broad potential of geodiversity in various scientific and applied fields. At the same time, the concept is still seeking wider recognition, both within geosciences and between geosciences and other disciplines. A major challenge is to explain geodiversity in a way that researchers from different disciplines can understand and agree upon. For example, within ecological discourse, geodiversity is often conflated with environmental heterogeneity, most likely due to the routine inclusion of abiotic environmental factors such as climate or topography in ecological research. Recognising geodiversity in ecological studies can help to appreciate the wide variation within the non-living environment and move towards a comprehensive understanding of natural diversity.

Translating geodiversity and its components between disciplines (e.g. geosciences and biosciences) requires unravelling geodiversity from the ground up (e.g. recognising its diversity as a geological, pedological, geomorphological and hydrological entity) and understanding different research perspectives (see also Maliniemi *et al.* 2024). Given the complex interactions between biotic and abiotic environments, increased collaboration between environmental disciplines is needed. Such collaboration not only facilitates progress within geodiversity research, but also extends its benefits to other fields where geodiversity could open up new, unexpected research avenues.

To bridge the gap between disciplines, I (among other geodiversity researchers) have drawn inspiration from ecological research and incorporated it into geodiversity research, highlighting the opportunities it offers. A key strategy for advancing both the conceptual and methodological aspects of geodiversity is to accept 'geodiversity' as analogous to 'biodiversity' (see also Gray 2021). Methodologically, the use of unified approaches to geodiversity and biodiversity assessment could prove beneficial for applied purposes such as nature conservation. It would also facilitate the extension of geodiversity–biodiversity research across different scales.

However, criticism of crude geodiversity assessment methods, such as the use of grid-based georichness indices, is not uncommon even among geodiversity researchers due to their lack of qualitative evaluation (see Gray 2021). However, given the broad and multidisciplinary nature of geodiversity, it is essential to consider multiple perspectives in its development. Drawing inspiration from adjacent disciplines is a prominent approach that is not new. Methods from biodiversity research have been used even earlier in pedodiversity research (Ibáñez *et al.* 1995). Exploring various assessment methods can uncover unexpected avenues of research and make geodiversity more approachable by providing familiar reference points, such as the parallel between species richness and georichness. In addition, extensive research on biodiversity indices provides valuable insights, including understanding the limitations of crude richness variables and identifying the best complementary options (e.g. Roswell *et al.* 2021).

At the same time, it is important to recognise that the crude assessment of geodiversity and its relationship to biodiversity should only be interpreted to a certain extent. For example, while I suggest that geodiversity could serve as a valuable tool for assessing the condition and conservation needs of water bodies and their catchments (Paper II), empirical studies to support or refute this claim are lacking, particularly with regard to the underlying mechanisms of the geodiversity–biodiversity relationship. Even though geodiversity provides a framework for freshwater conservation that can be applied to both water bodies and their catchments conceptually, more empirical studies are needed to confirm the link in different contexts. Similarly, the comparison of georichness and vascular plant species richness in Switzerland and Finland in Paper III relies solely on correlational data analysis. Nonetheless, even simple correlation studies are valuable at this relatively early stage of geodiversity research in order to better plan future studies.

Hopefully, the European geodiversity data (Paper III) will help to address some of the issues outlined above, such as establishing the concept of geodiversity and providing a basis for further empirical studies. Although the European geodiversity data represents a major effort and progress in large-scale geodiversity–biodiversity studies, it is not without limitations. It should be acknowledged that the data represents only one perspective of categorising and including geodiversity and different geofeatures. For instance, Hjort *et al.* (2024) discuss in length about the key development points in establishing a geodiversity taxonomy and alternative ways of categorising geofeatures, in addition to the perspectives that I have presented in Chapter 2.

The European dataset in Paper III is based on a limited set of variables that describe geodiversity. However, there are opportunities to explore additional options that might better capture the structural (e.g. geological substrate heterogeneity) and functional (e.g. soil chemical properties) aspects of geodiversity (see Table 1), and that can be based on characteristics other than the presence or absence of the geofeatures (see Figure 2). In addition, the relationship between alternative variables representing geology, pedology, geomorphology and hydrology should be further explored (see also discussion of alternative approaches in Alsbach *et al.* 2024).

There are few issues that should be acknowledged when using data from different sources, such as scale and harmonisation of data. In both Papers II and III, the original source data for geology, pedology, geomorphology and hydrology were collected and produced independently for specific purposes, each with its own spatial scale. This variability in the scales of the original data sources introduces uncertainty into the geodiversity assessments (see also discussion in Kaskela & Kotilainen 2017). For the European dataset (Paper III), we addressed this by selecting only data with an original resolution of <1-km. Notably, the hydrological data are at high spatial resolution (20 m), which is necessary for accurate mapping linear features such as rivers. Thematic resolution was ensured by including a relatively equal number or diverse representation of geofeatures per each geodiversity component (see also Wu 2004 and Buyantuev & Wu 2007 on thematic and spatial scales in landscape pattern analysis). Scale-related issues are also discussed in more detail in Paper III. Advances in more intensive geodiversity monitoring and data organisation would help to address many scale-related issues, but would also facilitate the integration of geodiversity into biodiversity investigations (see also Schrodt *et al.* 2019, 2024 on Essential Geodiversity Variables).

8.7 Themes for future research

This chapter explores four key themes for future research in the quantitative assessment of geodiversity in biodiversity surveys. These themes include refining the concept of geodiversity, improving methodological approaches to measuring geodiversity, expanding empirical evidence on the relationship between geodiversity and biodiversity, and establishing a robust data infrastructure for geodiversity information.

First, accepting geodiversity as analogous to biodiversity is a step towards clarifying the concept of geodiversity and harnessing the potential of geodiversity in biodiversity investigations. Additionally, breaking down the concept of geodiversity into clear, easily understood and measurable components would enhance its application in variety of research. The taxonomy of geodiversity is a step towards such clarification (see Hjort *et al.* 2024). Considering the sources of confusion in ecological discourse, there should be more discussion about the boundaries and dimensions of geodiversity and how it relates to concepts such as environmental heterogeneity and landscape diversity (e.g. Turner 1989; Stein *et al.* 2014). Given the potential of geodiversity as a landscape-scale conservation tool, promoting and refining the concept of geodiversity, particularly in this context, holds great promise for practical applications. In Norway, Simensen *et al.* (2021, 2022) have made extensive efforts to integrate geodiversity into such applications. Notably, while landscape-scale geodiversity was considered in the thesis through the spatial resolution of the quantitative assessment, different methodological approaches may define 'landscape-scale' differently.

Second, improving the methodological assessment of geodiversity is crucial for enhancing the accuracy, reliability, and applicability of geodiversity research. This process involves both refining existing techniques and exploring new methodologies with clearly defined objectives and instructions. Although there are several reviews of geodiversity assessment methods (e.g. Boothroyd & McHenry 2019; Brilha 2016; Crisp *et al.* 2021, 2022; Zwolinski *et al.* 2018), the growing interest in this field requires regular updates. This includes considering different perspectives of research—such as investigations on biodiversity, ecosystem and geosystem services or geoconservation—while separately considering quantitative, qualitative and integrated assessments. For quantitative assessment, in particular, it is important to develop and compare alternative methods, such as richness-based indices (e.g. georichness) and abundance-based or gradient-based indices (e.g. Shannon diversity index or beta diversity indices). This methodological development should align with the acceptance of geodiversity as an analogous concept to biodiversity, drawing on insights from ecological diversity research.

Furthermore, while standardised assessment protocols across different spatial and temporal scales are necessary to generate more reliable empirical evidence, methods may vary depending on contextual factors such as scale or ecosystem type (see also Chapter 4.2). While the general framework for geodiversity assessment may be universal, the execution may differ between local and global scale studies (e.g. conducting fieldwork vs. using GIS data). A clear and coherence methodological tool selection is essential to ensure consistent and meaningful results, as vague or scattered methodologies can undermine the integrity of research results and reduce research motivation.

Third, despite the well-reasoned theoretical framework linking geodiversity and biodiversity, a substantial gap persists in empirical evidence supporting this relationship (cf. Alahuhta *et al.* 2020). Considering the scattered nature of current knowledge, there is a need for more comparable empirical studies across different geographical regions, ecosystems, taxa and spatial and temporal scales. Simple assessment approaches could enhance the accessibility of geodiversity studies across different disciplines. While grid-based geodiversity assessment is feasible at larger scales, local-scale studies can provide deeper insights into the mechanisms underlying the geodiversity–biodiversity relationship. Attention should also be paid to the regional coverage of the studies (see e.g. Sayama 2024 on Eurocentricity), emphasizing the need for more global collaborations and perspectives.

Fourth, future research would benefit from a data infrastructure that supports geodiversity research and its practical implementation. Schrodt *et al.* (2024) extensively discuss this topic in the context of Essential Geodiversity Variables, highlighting the current challenge that geodiversity-related data are scattered, making them difficult to locate and use effectively. Similar observations were made during the data selection process for Paper III, and the lack of accurate, large-scale data was also noted by

Wolniewiz (2023) and Polman *et al.* (2024) in their European and global geodiversity assessments, respectively. Schrodt *et al.* (2024) also highlight another issue: while biodiversity databases such as GBIF and TRY contain extensive data on species occurrence and traits, they often lack accompanying environmental information. This reflects a biocentric bias in research and highlights the need for interdisciplinary collaboration. In addition, many databases have a spatial bias, with a predominant focus on Europe (e.g. Hughes *et al.* 2024). Although Zarnetske *et al.* (2019) and Schrodt *et al.* (2024) have provided some summaries of geodiversity data availability, these should be consolidated into easily accessible repositories to reach a wider audience. A future challenge is to harmonise the spatial and temporal scales of the data, possibly merging national datasets for this purpose.

9 Conclusions

The aim of this thesis was to provide theoretical and methodological premise for exploring landscape geodiversity in biodiversity investigations. Through a literature review in Paper I (Tukiainen *et al.* 2023), we identified current knowledge gaps in geodiversity–biodiversity research and emphasised the need for more empirical evidence and standardised research methods. In an empirical exploration in Paper II (Toivanen *et al.* 2019), we investigated the relationship between geodiversity and biodiversity in Finnish freshwaters—a context where such links are underexplored—and found a positive relationship between catchment geodiversity and aquatic plant species richness. These findings support the theoretical concept of geodiversity as a foundation for biodiversity and argue for its integration into freshwater conservation efforts. Therefore, in Paper III (Toivanen *et al.* 2024a), we provided Europe-wide geodiversity data to support future research and provide more empirical evidence on the contribution of geodiversity to biodiversity. We also provided guidelines for a commonly used grid-based approach, a quantitative assessment method suitable for large-scale geodiversity and biodiversity studies.

These contributions advance knowledge in geodiversity research and have practical implications for conservation practice, policy making and public perception. The academic implications highlight the contributions of the thesis to the advancement of knowledge and methodologies in geodiversity research. The applied implications emphasise the importance of integrating geodiversity into conservation practice, policy making and public perception.

9.1 Academic implications

This thesis strengthens the empirical evidence suggesting a positive relationship between geodiversity and biodiversity. Moreover, it highlights the interconnectedness between aquatic and terrestrial environments. These findings underscore the importance of considering geodiversity in biodiversity investigations and encourage its application in different contexts, such as different ecosystems.

Secondly, the thesis advocates for the development of corresponding assessment methods for geodiversity and biodiversity, such as georichness and species richness. Adopting assessment methods from biodiversity research offers a versatile selection of assessment methods with long research traditions, allowing for comparable perspectives to study both geodiversity and biodiversity. It also promotes equality between both the abiotic diversity and biotic diversity of nature.

Thirdly, the thesis establishes a landscape-scale quantitative approach to geodiversity assessment by providing tools and guidance for grid-based assessment. It provides a systematic framework for quantifying geodiversity from landscape to global scales, facilitating more standardised and reproducible research in the field.

Finally, by providing readily available geodiversity data and related methodology, the thesis facilitates Europe-wide geodiversity and geodiversity–biodiversity studies, to be extended across disciplines. This comprehensive dataset and methodology will allow researchers to conduct comparative analyses across different regions, ecosystems and spatial scales, which in turn will contribute to a deeper understanding of geodiversity patterns and their ecological implications on a larger scale.

9.2 Applied implications

The applied implications highlight the importance of recognising, integrating and valuing geodiversity in various aspects of conservation, policy making and public perception.

This thesis recommends systematically integrating geodiversity into nature conservation planning and efforts, highlighting synergies with biodiversity. By recognising the interconnectedness between geodiversity and biodiversity, we can make conservation strategies more comprehensive and effective in preserving a range of ecosystems and their functions. For instance, in freshwater assessments and restoration projects, it is crucial to consider the entire catchment area, including how restoration activities affect both aquatic and terrestrial biodiversity and ecosystem functions across the catchment.

Geodiversity is often overlooked and reduced to mere natural resources in everyday conversations and policy making, neglecting its integral role in natural diversity (see also Gray 2018). This perspective fails to appreciate the diverse aspects of geodiversity and their contributions to various ecosystem and geosystem functions, which directly benefit human well-being. By presenting geodiversity as an equal component of nature's diversity with biodiversity, we aim to broaden perspectives and advocate for its inclusion in policy and conservation initiatives.

In conclusion, this thesis suggests a re-evaluation of how we perceive natural diversity in our daily lives. By highlighting the multifaceted nature of geodiversity and its inherent connection to biodiversity, this thesis challenges conventional views that define diversity narrowly and primarily in biotic terms. Then again, it is often the mountainous landscapes and murmuring brooks that attract our attention outdoors, revealing the hidden appreciation of geodiversity. Embracing a broader perspective of nature's diversity can offer a gateway to a more holistic understanding of our surroundings, inspiring a deeper appreciation and consideration of geodiversity.

References

Alahuhta J, Luukinoja J, Tukiainen H & Hjort J (2016) Importance of spatial scale in structuring emergent lake vegetation across environmental gradients and scales: GIS-based approach. *Ecological Indicators* 60: 1164–1172. https://doi.org/10.1016/j.ecolind.2015.08.045

Alahuhta J, Ala-Hulkko T, Tukiainen H, Purola L, Akujärvi A, Lampinen R & Hjort J (2018) The role of geodiversity in providing ecosystem services at broad scales. *Ecological Indicators* 91: 47–56. https://doi.org/10.1016/j.ecolind.2018.03.068

Alahuhta J, Toivanen M & Hjort J (2020) Geodiversity–biodiversity relationship needs more empirical evidence. *Nature Ecology & Evolution* 4: 2–3. https://doi.org/10.1038/s41559-019-1051-7

Alahuhta J, Tukiainen H, Toivanen M, Ala-Hulkko T, Farrahi V, Hjort J, Ikäheimo TM, Lankila T, Maliniemi T, Puhakka S, Salminen H, Seppänen M, Korpelainen R & Ding D (2023) Acknowledging geodiversity in safeguarding biodiversity and human health. *The Lancet Planetary Health* 6: E987–E992. https://doi.org/10.1016/S2542-5196(22)00259-5

Alahuhta J, García-Girón J, Hjort J, Salminen H, Tukiainen H & Heino J (2024) Quantitative measurement of geodiversity uniqueness: research implications and conservation applications. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 382: 20230056. https://doi.org/10.1098/rsta.2023.0056

Albano CM (2015) Identification of geophysically diverse locations that may facilitate species' persistence and adaptation to climate change in the southwestern United States. *Landscape Ecology* 30(6): 1023–1037. https://doi.org/10.1007/s10980-015-0167-7

Alsbach CME, Seijmonsbergen AC & Hoorn C (2024) Geodiversity in the Amazon drainage basin. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 382: 20230065. https://doi.org/10.1098/rsta.2023.0065

Amatulli G, McInerney D, Sethi T, Strobl P & Domisch S (2020) Geomorpho90m, empirical evaluation and accuracy assessment of global high-resolution geomorphometric layers. *Scientific Data* 7: 162. https://doi.org/10.1038/s41597-020-0479-6

Anderson MG & Ferree CE (2010) Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE* 5(10): e11554. https://doi.org/10.1371/journal.pone.0011554

Anougmar S, Meesters A, van Ree D & Compernolle T (2024) The dilemma of valuing geodiversity: geoconservation versus geotourism. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 382: 20230049. https://doi.org/10.1098/rsta.2023.0049

Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A, Muellner-Riehl AN, Kreft H, Linder HP, Badgley C, Fjeldså J, Fritz SA, Rahbek C, Herman F, Hooghiemstra H & Hoorn C (2018) Geological and climatic influences on mountain biodiversity. *Nature Geoscience* 11: 718–725. https://doi.org/10.1038/s41561-018-0236-z

Araujo AM & Pereira DÍ (2018) A new methodological contribution for the geodiversity assessment: Applicability to Ceará State (Brazil). *Geoheritage* 10(4): 591–605. https://doi.org/10.1007/s12371-017-0250-3

Bailey JJ, Boyd DS, Hjort J, Lavers CP & Field R (2017) Modelling native and alien vascular plant species richness: At which scales is geodiversity most relevant? *Global Ecology and Biogeography* 26: 763–776. https://doi.org/10.1111/geb.12574

Bailey JJ, Boyd DS & Field R (2018) Models of upland species' distributions are improved by accounting for geodiversity. *Landscape Ecology* 33(12): 2071–2087. https://doi.org/10.1007/s10980-018-0723-z

Bailey J, Field R, van Ree D & Schrodt F (2024) Geodiversity for science and society. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 382: 20230062. https://doi.org/10.1098/rsta.2023.0062

Barton K (2017) *MuMIn: Multi-model inference.* R package version 1.40.0. https://CRAN.R-project.org/package=MuMIn

Batlle JRM & van der Hoek Y (2021) Plant community associations with morpho-topographic, geological and land use attributes in a semi-deciduous tropical forest of the Dominican Republic. *Neotropical Biodiversity* 7(3): 465–475. https://doi.org/10.1080/23766808.2021.1987769

Beier P, Hunter ML & Anderson M (2015) Introduction. *Conservation Biology* 29(3): 613–617. https://doi.org/10.1111/cobi.12511

Benedetti Y, Callaghan CT, Ulbrichová I, Galanaki A, Kominos T, Abou Zeid F, Ibáñez-Álamo JD, Suhonen J, Díaz M, Markó G, Bussière R, Tryjanowski P, Bukas N, Mägi M, Leveau L, Pruscini F, Jerzak L, Ciebiera O, Jokimäki J, Kaisanlahti-Jokimäki ML & Møller AP (2023) EVI and NDVI as proxies for multifaceted avian diversity in urban areas. *Ecological Applications* 33(3): e2808. https://doi.org/10.1002/eap.2808

Benito-Calvo A, Pérez-González A, Magri O & Meza P (2009) Assessing regional geodiversity: The Iberian Peninsula. *Earth Surface Processes and Landforms* 34(10): 1433–1445. https://doi.org/10.1002/esp.1840

Bétard F & Peulvast JP (2019) Geodiversity hotspots: Concept, method and cartographic application for geoconservation purposes at a regional scale. *Environmental Management* 63(6): 822–834. https://doi.org/10.1007/s00267-019-01168-5

Bollati I, Leonelli G, Vezzola L & Pelfini M (2015) The role of ecological value in geomorphosite assessment for the debris-covered Miage Glacier (Western Italian Alps) based on a review of 2.5 centuries of scientific study. *Geoheritage* 7(2): 119–135. https://doi.org/10.1007/s12371-014-0111-2

Boothroyd A & McHenry M (2019) Old processes, new movements: The inclusion of geodiversity in biological and ecological discourse. *Diversity* 11(11): 216. https://doi.org/10.3390/d11110216

Bradbury J (2014) A keyed classification of natural geodiversity for land management and nature conservation purposes. *Proceedings of the Geologists' Association* 125(3): 329–349. https://doi.org/10.1016/j.pgeola.2014.03.006

Bressan D (2012) Darwin the geologist. *Scientific American*, 12 February 2012. https://www.scientificamerican.com/blog/history-of-geology/darwin-the-geologist/ (accessed 15 May 2024)

Brilha J (2016) Inventory and quantitative assessment of geosites and geodiversity sites: A review. *Geoheritage* 8: 119–134. https://doi.org/10.1007/s12371-014-0139-3

Brilha J, Gray M, Pereira DI & Pereira P (2018) Geodiversity: An integrative review as a contribution to the sustainable management of the whole of nature. *Environmental Science & Policy* 86: 19–28. https://doi.org/10.1016/j.envsci.2018.05.001

Brocx M & Wetlands Research Association (2008) *Geoheritage: From global perspectives to local principles for conservation and planning (vol. 15).* Western Australian Museum, Welshpool, WA.

Brost BM & Beier P (2012) Use of land facets to design linkages for climate change. *Ecological Applications* 22: 87–103. https://doi.org/10.1890/11-0213.1

Brucet S, Poikane S, Lyche-Solheim A & Birk S (2013) Biological assessment of European lakes: Ecological rationale and human impacts. *Freshwater Biology* 58(6): 1106–1115. https://doi.org/10.1111/fwb.12111

Burnett MR, August PV, Brown JH & Killingbeck KT (1998) The influence of geomorphological heterogeneity on biodiversity I. A patch-scale perspective. *Conservation Biology* 12(2): 363–370. https://doi.org/10.1111/j.1523-1739.1998.96238.x

Burnham K & Anderson D (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research* 33: 261–304. https://doi.org/10.1177/0049124104268644

Buyantuyev A & Wu J (2007) Effects of thematic resolution on landscape pattern analysis. *Landscape Ecology* 22(1): 7–13. https://doi.org/10.1007/s10980-006-9010-5

Börker J, Hartmann J, Amann T & Romero-Mujalli G (2018) Terrestrial sediments of the earth: Development of a global unconsolidated sediments map database (GUM). *Geochemistry, Geophysics, Geosystems* 19: 997–1024. https://doi.org/10.1002/2017GC007273

Cary Institute of Ecosystem Studies (2024) *Definition of Ecology*. https://www.caryinstitute.org/news-insights/2-minute-science/definition-ecology (accessed 15 May 2024)

Cervellini M, Zannini P, Di Musciano M, Fattorini S, Jiménez-Alfaro B, Rocchini D, Field R, R. Vetaas O, Irl SD.H, Beierkuhnlein C, Hoffmann S, Fischer J-C, Casella L, Angelini P, Genovesi P, Nascimbene J & Chiarucci A (2020) A grid-based map for the Biogeographical Regions of Europe. *Biodiversity Data Journal* 8: e53720. https://doi.org/10.3897/BDJ.8.e53720

Chakraborty A & Gray M (2020) A call for mainstreaming geodiversity in nature conservation research and praxis. *Journal for Nature Conservation* 56: 125862. https://doi.org/10.1016/j.jnc.2020.125862

Claudino-Sales V (2021) Geodiversity and geoheritage in the perspective of geography. *Bulletin of Geography. Physical Geography Series* 21: 45–52. https://doi.org/10.2478/bgeo-2021-0008

Comer PJ, Pressey RL, Hunter ML Jr., Schloss CA, Buttrick SC, Heller NE, Tirpak JM, Faith DP, Cross MS & Shaffer ML (2015) Incorporating geodiversity into conservation decisions. *Conservation Biology* 29(3): 692–701. https://doi.org/10.1111/cobi.12508

Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Costello MJ, Basher Z, Sayre R, Breyer S & Wright DJ (2018) Stratifying ocean sampling globally and with depth to account for environmental variability. *Scientific Reports* 8: 11259. https://doi.org/10.1038/s41598-018-29419-1

Crisp JR, Ellison JC & Fischer A (2021) Current trends and future directions in quantitative geodiversity assessment. *Progress in Physical Geography: Earth and Environment* 45(4): 514–540. https://doi.org/10.1177/0309133320967219

Crisp JR, Ellison JC, Fischer A & Tan JS (2022) Geodiversity inclusiveness in biodiversity assessment. *Progress in Physical Geography: Earth and Environment* 47(3): 414-437. https://doi.org/10.1177/03091333221122292

Crisp JR, Ellison JC & Fischer A (2023) Omnidiversity consolidation of conservation assessment: A case study of Tasmanian coastal geoconservation sites. *Geoconservation Research* 5(1): 108–134. https://doi.org/10.30486/gcr.2022.1947195.1099

Crofts R, Gordon JE, Brilha J, Gray M, Gunn J, Larwood J, Santucci VL, Tormey D & Worboys GL (2020) Guidelines for geoconservation in protected and conserved areas. *Best Practice Protected Area Guidelines Series* 31. IUCN, Gland, Switzerland. https://doi.org/10.2305/IUCN.CH.2020.PAG.31.en

Crowther TW, van den Hoogen J, Wan J, Mayes MA, Keiser AD, Mo L, Averill C & Maynard DS (2019) The global soil community and its influence on biogeochemistry. *Science* 365: eaav0550. https://doi.org/10.1126/science.aav0550

da Silva MLN, do Nascimento MAL & Mansur KL (2019) Quantitative assessments of geodiversity in the area of the Seridó Geopark Project, Northeast Brazil: Grid and centroid analysis. *Geoheritage* 11: 1177–1186. https://doi.org/10.1007/s12371-019-00368-z

Dakhil MA, Li J, Pandey B, Pan K, Liao Z, Olatunji OA, Zhang L, Eid EM & Abdelaal M (2021) Richness patterns of endemic and threatened conifers in south-west China: Topographic-soil fertility explanation. *Environmental Research Letters* 16(3): 034017. https://doi.org/10.1088/1748-9326/abda6e

De Falco N, Tal-Berger R, Hjazin A, Yizhaq H, Stavi I & Rachmilevitch S (2021) Geodiversity impacts plant community structure in a semi-arid region. *Scientific Reports* 11: 15259. https://doi.org/10.1038/s41598-021-94698-0

de Paula Silva J, Alves GB, Ross JLS, Oliveira FS, Nascimento MAL, Felini MG, Manosso FC & Pereira DI (2021) The Geodiversity of Brazil: Quantification, Distribution, and Implications for Conservation Areas. *Geoheritage* 13: 75. https://doi.org/10.1007/s12371-021-00598-0

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD & Gorné LD (2016) The global spectrum of plant form and function. *Nature* 529: 167–171. https://doi.org/10.1038/nature16489

Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K & Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* 104(52): 20684–20689. https://doi.org/10.1073/pnas.0704716104

Dolan MFJ, Bøe R & Bjarnadóttir LR (2022) Delivering seabed geodiversity information through multidisciplinary mapping initiatives: Experiences from Norway. *GEUS Bulletin* 52. https://doi.org/10.34194/geusb.v52.8325

dos Santos DS, Mansur KL, de Arruda Jr ER, Dantas ME & Shinzato E (2019) Geodiversity mapping and relationship with vegetation: A regional-scale application in SE Brazil. *Geoheritage* 11: 399–415. https://doi.org/10.1007/s12371-018-0295-y

Dudley N (ed.) (2008) *Guidelines for Applying Protected Area Management Categories*. IUCN, Gland, Switzerland. https://portals.iucn.org/library/sites/library/files/documents/PAG-021.pdf (accessed 15 May 2024)

Duscher K, Günther A, Richts A, Clos P, Philipp U & Struckmeier W (2015) The GIS layers of the "International Hydrogeological Map of Europe 1:1,500,000" in a vector format. *Hydrogeology Journal* 23: 1867–1875. https://doi.org/10.1007/s10040-015-1296-4

EEA, European Environment Agency. (2013). *EEA reference grid*. https://www.eea.europa.eu/ds_resolveuid/58565fd7fb744fec9a546f7db6c5146e (accessed 13 April 2022)

EEA, European Environment Agency. (2016). *European Digital Elevation Model (EU-DEM), version 1.1*. https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1?tab=download (accessed 9 February 2023)

EEA, European Environment Agency. (2019). *EU-Hydro – River Network Database, version 1.3*. https://land.copernicus.eu/imagery-in-situ/eu-hydro/eu-hydro-river-network-database (accessed 13 April 2022).

EEA, European Environment Agency. (2020). *Corine Land Cover (CLC) 2018, version 2020_20u1*. Retrieved from https://land.copernicus.eu/pan-european/corine-land-cover/clc2018 (accessed 15 February 2022).

EEA, European Environment Agency. (2023). *High Resolution Snow and Ice Monitoring: Persistent Snow Area*. https://www.eea.europa.eu/en/datahub/datahubitem-view/603f419b-f9ca-4642-b043-4a333cc91b02 (accessed 15 May 2024).

Elith J, Leathwick JR & Hastie T (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Erikstad L, Bakkestuen V, Dahl R, Arntsen ML, Margreth A, Angvik TL & Wickström L (2022) Multivariate analysis of geological data for regional studies of geodiversity. *Resources* 11(6): 51. https://doi.org/10.3390/resources11060051

ESRI (2021) *ArcGIS Pro desktop, version 2.8*. Environmental Systems Research Institute, Redlands, CA.

Esri (2024a) *Zonal Statistics as Table* (Spatial Analyst). Retrieved from https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/zonal-statistics-as-table.htm (accessed 15 May 2024).

Esri (2024b) *Tabulate Area* (Spatial Analyst). Retrieved from https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/tabulate-area.htm (accessed 15 May 2024).

Fan Y, Li H & Miguez-Macho G (2013) Global patterns of groundwater table depth. *Science* 339: 940–943. https://doi.org/10.1126/science.1229881

FBIF, Finnish Biodiversity Information Facility. (2023). *Kastikka Floristic Archives (Kastikka Ark).* Occurrence dataset. https://doi.org/10.15468/kasmwk (accessed via GBIF.org on 2 October 2023).

FBIF, Finnish Biodiversity Information Facility. (2024). *Yhtenäiskoordinaatisto (YKJ).* https://laji.fi/about/5310 (accessed 15 May 2024). [In Finnish]

Ferrer-Valero N, Hernández-Calvento L & Hernández-Cordero AI (2019) Insights of long-term geomorphological evolution of coastal landscapes in hot-spot oceanic islands. *Earth Surface Processes and Landforms* 44: 565–580. https://doi.org/10.1002/esp.4518

Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM & Turner JRG (2009) Spatial species-richness gradients across scales: A meta-analysis. *Journal of Biogeography* 36: 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

Finnish Environment Institute. (2013). *Pohjavesialueet (Groundwater bodies).* https://ckan.ymparisto.fi/dataset/%7B8F45F7BF-669F-4434-A8DB-8E686933F6FF%7D (accessed 15 May 2024).

Finnish Environment Institute. (2015). *Vesipuitedirektiivin mukaiset vesimuodostumat (Water bodies according to Water Framework Directive).* https://ckan.ymparisto.fi/dataset/%7BA3748B80-6E63-4460-A8B7-72CB9884F69B%7D (accessed 15 May 2024).

Finnish Environment Institute. (2016/2024). *Avoimet ympäristötietojärjestelmät.* https://www.syke.fi/fi-FI/Avoin_tieto/Ymparistotietojarjestelmat (original data accessed and retrieved in 2016, referenced link accessed 15 May 2024)

Finnish Environment Institute. (2021). *Ranta10 - rantaviiva 1:10 000.* https://ckan.ymparisto.fi/dataset/ranta10-rantaviiva-1-10-000 (accessed 22 July 2024)

Forte JP, Brilha J, Pereira DI & Nolasco M (2018) Kernel density applied to the quantitative assessment of geodiversity. *Geoheritage* 10: 205–217. https://doi.org/10.1007/s12371-018-0282-3

Fox N, Graham LJ, Eigenbrod F, Bullock JM & Parks KE (2020) Incorporating geodiversity in ecosystem service decisions. *Ecosystems and People* 16(1): 151–159. https://doi.org/10.1080/26395916.2020.1758214

Geological Survey of Finland (2010a) *Kallioperä 1:200 000 / Bedrock of Finland 1:200 000.* https://tupa.gtk.fi/paikkatieto/meta/bedrock_of_finland_200k.html

Geological Survey of Finland (2010b) *Maaperä 1:200 000 (maalajit)/Superficial deposits of Finland 1:200 000 (sediment polygons).* https://tupa.gtk.fi/paikkatieto/meta/maapera_200k.html

Gerstner BE, Blair ME, Bills P, Cruz-Rodriguez CA & Zarnetske PL (2024) The influence of scale-dependent geodiversity on species distribution models in a biodiversity hotspot. *Philosophical Transactions of the Royal Society A* 382: 20230057. https://doi.org/10.1098/rsta.2023.0057

Gonçalves J, Mansur K, Santos D, Henriques R & Pereira P (2022) Is it worth assessing geodiversity numerically? A comparative analysis between quantitative and qualitative approaches in Miguel Pereira Municipality, Rio de Janeiro, Brazil. *Geosciences* 12(9): 347. https://doi.org/10.3390/geosciences12090347

Gordon JE, Brazier V, Thompson DBA & Horsfield D (2001) Geo-ecology and the conservation management of sensitive upland landscapes in Scotland. *CATENA* 42(2–4): 323-332. https://doi.org/10.1016/S0341-8162(00)00144-2

Gordon JE & Barron HF (2012) Valuing geodiversity and geoconservation: Developing a more strategic ecosystem approach. *Scottish Geographical Journal* 128(3–4): 278–297. https://doi.org/10.1080/14702541.2012.725861

Gordon JE, Bailey JJ & Larwood JG (2022) Conserving nature's stage provides a foundation for safeguarding both geodiversity and biodiversity in protected and conserved areas. *Parks Stewardship Forum* 38(1): 46–55. https://doi.org/10.5070/P538156118

Gray M (2008a) Geoheritage 1. Geodiversity: A new paradigm for valuing and conserving geoheritage. *Geoscience Canada* 35(2): 51–59. https://id.erudit.org/iderudit/geocan35_2ser01

Gray M (2008b) Geodiversity: Developing the paradigm. *Proceedings of the Geologists' Association* 119(3–4): 287-298. https://doi.org/10.1016/S0016-7878(08)80307-0

Gray M (2013) *Geodiversity: Valuing and conserving abiotic nature* (2nd ed.). Wiley-Blackwell.

Gray M (2018) The confused position of the geosciences within the "natural capital" and "ecosystem services" approaches. *Ecosystem Services* 34(Part A): 106–112. https://doi.org/10.1016/j.ecoser.2018.10.010

Gray M (2021) Geodiversity: A significant, multi-faceted and evolving geoscientific paradigm rather than a redundant term. *Proceedings of the Geologists' Association* 132(5): 605–619. https://doi.org/10.1016/j.pgeola.2021.09.001

Guisan A & Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135(2–3): 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Halvorsen R, Skarpaas O, Bryn A, Bratli H, Erikstad L, Simensen T & Lieungh E (2020) Towards a systematics of ecodiversity: The EcoSyst framework. *Global Ecology and Biogeography* 29: 1887–1906. https://doi.org/10.1111/geb.13164

Hartmann J & Moosdorf N (2012) The new global lithological map database GLiM: A representation of rock properties at the Earth surface. *Geochemistry, Geophysics, Geosystems* 13: Q12004. https://doi.org/10.1029/2012GC004370

Hastie T, Tibshirani R, & Friedman J (2001) The elements of statistical learning: Data mining, inference, and prediction. Springer-Verlag, New York.

Hawkins BA, Porter EE & Diniz-Filho JAF (2003) Productivity and history as predictors of the latitudinal diversity gradient for terrestrial birds. *Ecology* 84: 1608–1623.

Heino J, Alahuhta J & Fattorini S (2019) Macroecology of ground beetles: Species richness, range size and body size show different geographical patterns across a climatically heterogeneous area. *Journal of Biogeography* 46: 2548–2557. https://doi.org/10.1111/jbi.13693

Heino J, Alahuhta J, Bini LM, Cai Y, Heiskanen A-S, Hellsten S, Kortelainen P, Kotamäki N, Tolonen KT, Vihervaara P, Vilmi A & Angeler DG (2021) Lakes in the era of global change: Moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biological Reviews* 96: 89–106. https://doi.org/10.1111/brv.12647

Heino J & Koljonen S (2022) A roadmap for sustaining biodiversity and ecosystem services through joint conservation and restoration of northern drainage basins. *Ecological Solutions and Evidence* 3: e12142. https://doi.org/10.1002/2688-8319.12142

Heino J, Toivanen M & Alahuhta J (2023) Deciphering land-use influences on boreal lakes to guide landscape planning. *Ecological Solutions and Evidence* 4: e12242. https://doi.org/10.1002/2688-8319.12242

Hengl T (2006) Finding the right pixel size. *Computers & Geosciences* 32(9): 1283–1298. https://doi.org/10.1016/j.cageo.2005.11.008

Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, Blagotić A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B, Guevara MA, Vargas R, MacMillan RA, Batjes NH, Leenaars JGB, Ribeiro E, Wheeler I, Mantel S & Kempen B (2017) SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE* 12(2): e0169748. https://doi.org/10.1371/journal.pone.0169748

Hjort J & Luoto M (2010) Geodiversity of high-latitude landscapes in northern Finland. *Geomorphology* 115(1–2): 109–116. https://doi.org/10.1016/j.geomorph.2009.09.039

Hjort J, Heikkinen RK & Luoto M (2012) Inclusion of explicit measures of geodiversity improve biodiversity models in a boreal landscape. *Biodiversity and Conservation* 21: 3487–3506. https://doi.org/10.1007/s10531-012-0376-1

Hjort J, Gordon JE, Gray M & Hunter ML Jr (2015) Why geodiversity matters in valuing nature's stage. *Conservation Biology* 29: 630–639. https://doi.org/10.1111/cobi.12510

Hjort J, Tukiainen H, Salminen H, Kemppinen J, Kiilunen P, Snåre H, Alahuhta J & Maliniemi T (2022) A methodological guide to observe local-scale geodiversity for biodiversity research and management. *Journal of Applied Ecology* 59: 1756–1768. https://doi.org/10.1111/1365-2664.14183

Hjort J, Seijmonsbergen AC, Kemppinen J, Tukiainen H, Maliniemi T, Gordon JE, Alahuhta J & Gray M (2024) Towards a taxonomy of geodiversity. *Philosophical Transactions of the Royal Society A* 382: 20230060. https://doi.org/10.1098/rsta.2023.0060

Huggett R (1995) *Geoecology: An Evolutionary Approach*. 1st edition. Routledge. https://doi.org/10.4324/9780203138717

Hughes AC, Orr MC, Ma K, Costello MJ, Waller J, Provoost P, Yang Q, Zhu C & Qiao H (2021) Sampling biases shape our view of the natural world. *Ecography* 44: 1259–1269. https://doi.org/10.1111/ecog.05926

Hulshof CM & Spasojevic MJ (2020) The edaphic control of plant diversity. *Global Ecology and Biogeography* 29: 1634–1650. https://doi.org/10.1111/geb.13151

Hunter ML Jr, Jacobson GL Jr & Webb T III (1988) Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2: 375–385. https://doi.org/10.1111/j.1523-1739.1988.tb00202.x

Ibáñez JJ, De-Alba S, Bermúdez FF & García-Álvarez A (1995) Pedodiversity: Concepts and measures. *Catena* 24(3): 215–232. https://doi.org/10.1016/0341-8162(95)00028-Q

Ibáñez JJ, De-Alba S, Lobo A & Zucarello V (1998) Pedodiversity and global soil patterns at coarse scales (with discussion). *Geoderma* 83(3–4): 171–192. https://doi.org/10.1016/S0016-7061(97)00147-X

Ibáñez JJ, Brevik EC & Cerdá A (2019) Geodiversity and geoheritage: Detecting scientific and geographic biases and gaps through a bibliometric study. *Science of The Total Environment* 659(1): 1032–1044. https://doi.org/10.1016/j.scitotenv.2018.12.443

Ibáñez JJ & Brevik E C (2022) Geodiversity research at the crossroads: Two sides of the same coin. *Spanish Journal of Soil Science* 12: 10456. https://doi.org/10.3389/sjss.2022.10456

IPBES (2019) *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Díaz S, Settele J, Brondízio E S, ..., Zayas C N (eds.) IPBES Secretariat, Bonn, Germany. https://zenodo.org/doi/10.5281/zenodo.3553458

IUSS Working Group WRB (2022) *World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps* (4th edition). International Union of Soil Sciences (IUSS), Vienna, Austria. https://www.isric.org/sites/default/files/WRB_fourth_edition_2022-12-18.pdf

Jasiwicz J & Stepinski TF (2013) Geomorphons — a pattern recognition approach to classification and mapping of landforms. *Geomorphology* 182: 147–156. https://doi.org/10.1016/j.geomorph.2012.11.005

Jenny H (1941) *Factors of soil formation: a system of quantitative pedology*. Dover Publications, Inc, New York. https://soilandhealth.org/wp-content/uploads/01aglibrary/010159.Jenny.pdf (accessed 15 May 2024)

Jetz W, McGeoch MA, Guralnick R, Ferrier S, Beck J, Costello MJ, Fernandez M, Geller GN, Keil P, Merow C, Meyer C, Muller-Karger FE, Pereira HM, Regan EC, Schmeller DS & Turak E (2019) Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology & Evolution* 3: 539–551. https://doi.org/10.1038/s41559-019-0826-1

Johansson CE (2000) *Geodiversitet i nordisk naturvård* [Geodiversity in Nordic nature conservation]. Nordisk Ministerråd.

Johnson L, Richards C, Host G & Arthur J (1997) Landscape influences on water chemistry in Midwestern stream ecosystems. *Freshwater Biology* 37: 193–208. https://doi.org/10.1046/j.1365-2427.1997.d01-539.x

Jutzi M, Vilpert M, Juillerat P & Eggenberg S (2023) *Swiss National Databank of Vascular Plants*. Version 1.14. Swiss National Biodiversity Data and Information Centres – infospecies.ch. Occurrence dataset. https://doi.org/10.15468/7jffp3 (accessed via GBIF.org on 2 October 2023).

Karger DN, Lange S, Hari C, Reyer CPO & Zimmermann NE (2021) *CHELSA-W5E5 v1.0: W5E5 v1.0 downscaled with CHELSA v2.0*. ISIMIP Repository. https://doi.org/10.48364/ISIMIP.836809

Kaskela AM & Kotilainen AT (2017) Seabed geodiversity in a glaciated shelf area, the Baltic Sea. *Geomorphology* 295: 419–435. https://doi.org/10.1016/j.geomorph.2017.07.014

Kaskela AM, Rousi H, Ronkainen M, Orlova M, Babin A, Gogoberidze G, Kostamo K, Kotilainen AT, Neevin I, Ryabchuk D, Sergeev A & Zhamoida V (2017) Linkages between benthic assemblages and physical environmental factors: The role of geodiversity in Eastern Gulf of Finland ecosystems. *Continental Shelf Research* 142: 1–13. https://doi.org/10.1016/j.csr.2017.06.005

Kaskela AM & Kotilainen AT (2024) Quantifying seabed geodiversity of the Archipelago Sea, Baltic Sea, Finland. *GEUS Bulletin* 52. https://doi.org/10.34194/geusb.v52.8317

Keith DA (2011) Relationships between geodiversity and vegetation in south-eastern Australia. *Proceedings of the Linnean Society of New South Wales* 132: 5–26. https://biostor.org/reference/252238

Keith DA, Ferrer-Paris JR, Nicholson E, Bishop MJ, Polidoro BA, Ramirez-Llodra E, Tozer MG, Nel JL, Mac Nally R, Gregr EJ, Watermeyer KE, Essl F, Faber-Langendoen D, Franklin J, Lehmann CER, Etter A, Roux DJ, Stark JS, Rowland JA, Brummitt NA, Fernandez-Arcaya UC, Suthers IM, Wiser SK, Donohue I, Jackson LJ, Pennington RT, Iliffe TM, Gerovasileiou V, Giller P, Robson BJ, Pettorelli N, Andrade A, Lindgaard A, Tahvanainen T, Terauds A, Chadwick MA, Murray NJ, Moat J, Pliscoff P, Zager I & Kingsford RT (2022) A function-based typology for Earth's ecosystems. *Nature* 610: 513–518. https://doi.org/10.1038/s41586-022-05318-4

Kingsland SE (1991) Defining ecology as a science. *In* Real LA & Brown JH (eds.) *Foundations of Ecology: Classic Papers with Commentaries*, 1–13. University of Chicago Press, Chicago. https://uvic470ecology.weebly.com/uploads/1/2/4/4/12445281/definingscience.kingsland.1991.pdf

Knudson C, Kay K & Fisher S (2018) Appraising geodiversity and cultural diversity approaches to building resilience through conservation. *Nature Climate Change* 8: 678–685. https://doi.org/10.1038/s41558-018-0188-8

Kolada A (2016) The use of helophytes in assessing eutrophication of temperate lowland lakes: Added value? *Aquatic Botany* 129: 44–54. https://doi.org/10.1016/j.aquabot.2015.12.002

Kärnä O-M, Heino J, Grönroos M & Hjort J (2018) The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity. *Ecological Indicators* 94(1): 420–429. https://doi.org/10.1016/j.ecolind.2018.06.034

Kärnä O-M, Heino J, Laamanen T, Jyrkänkallio-Mikkola J, Pajunen V, Soininen J, Tolonen KT, Tukiainen H & Hjort J (2019) Does catchment geodiversity foster stream biodiversity? *Landscape Ecology* 34: 2469–2485. https://doi.org/10.1007/s10980-019-00901-z

Lacoul P & Freedman B (2006) Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews* 14(2): 89–136. https://doi.org/10.1139/a06-001

Lahti T & Lampinen R (2022) *Kasviatlas kaipaa tekijöitä: Atlas of the vascular flora of Finland: a review. Lutukka* 38(1): 30–37. http://hdl.handle.net/10138/352722 [In Finnish]

Lampinen R & Lahti T (2021) *Kasviatlas 2020*. Helsingin Yliopisto, Luonnontieteellinen keskusmuseo, Helsinki. http://kasviatlas.fi

Lausch A, Selsam P, Pause M & Bumberger J (2024) Monitoring vegetation-and geodiversity with remote sensing and traits. *Philosophical Transactions of the Royal Society A* 382: 20230058. https://doi.org/10.1098/rsta.2023.0058

Lawler JJ, Ackerly DD, Albano CM, Anderson MG, Dobrowski SZ, Gill JL, Heller NE, Pressey RL, Sanderson EW & Weiss SB (2015) The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology* 29: 618–629. https://doi.org/10.1111/cobi.12505

Legendre P & Legendre L (2012) *Numerical ecology* (2nd edition). Elsevier, Amsterdam.

Lehner B, Verdin K & Jarvis A (2008) New Global Hydrography Derived from Spaceborne Elevation Data. *Eos, Transactions, American Geophysical Union* 89(10): 93–94. https://doi.org/10.1029/2008EO100001

Leka J, Valta-Hulkkonen K, Kanninen A, Partanen S, Hellsten S, Ustinov A, Ilvonen R & Airaksinen O (2003) Vesimakrofyytit järvien ekologisen tilan arvioinnissa ja seurannassa. Maastomenetelmien ja ilmakuvatukinnan käyttökelpoisuuden arviointi Life Vuoksi -projektissa. *Alueelliset ympäristöjulkaisut* 312. https://urn.fi/URN:ISBN:952-11-1457-6

Lomolino MV, Riddle BR & Whittaker RJ (2016) *Biogeography* (5th edition). Oxford University Press.

Lopes C, Teixeira Z, Pereira DI & Pereira P (2023) Identifying optimal cell size for geodiversity quantitative assessment with richness, diversity and evenness indices. *Resources* 12(6): 65. https://doi.org/10.3390/resources12060065

Maliniemi T, Tukiainen H, Hjort J, Toivanen M, Vernham G, Bailey JJ, Baines O, Benniston L, Brilha J, Field R, Fox N, Gray M, Grytnes JA, Huusko K, Kemppinen J, Pereira P, Salminen H, Schrodt F, Turner L & Alahuhta J (2024) Too much diversity—Multiple definitions of geodiversity hinder its potential in biodiversity research. *Diversity and Distributions* 30: e13843. https://doi.org/10.1111/ddi.13843

McBratney A & Minasny B (2007) On measuring pedodiversity. *Geoderma* 141(1–2): 149–154. https://doi.org/10.1016/j.geoderma.2007.05.012

McGarigal K, Cushman SA, Neel MC & Ene E (2002*) FRAGSTATS: Spatial pattern analysis program for categorical maps*. Computer software program produced by the authors at the University of Massachusetts, Amherst. https://www.researchgate.net/publication/259011515_FRAGSTATS_Spatial_pattern_analysis_program_for_categorical_maps

Miller SN, Beier P & Albuquerque FS (2024) A test of conserving nature's stage: Protecting a diversity of geophysical traits can also support a diversity of species at a landscape scale. *Philosophical Transactions of the Royal Society A* 382: 20230063. https://doi.org/10.1098/rsta.2023.0063

Moilanen A, Leathwick J & Elith J (2008) A method for spatial freshwater conservation prioritization. *Freshwater Biology* 53: 577–592. https://doi.org/10.1111/j.1365-2427.2007.01906.x

MOT Oxford Dictionary of English (2024) *Landscape*. https://www.sanakirja.fi/l_oxford_english/english-english/landscape (accessed 12 August 2024)

Muellner-Riehl AN, Schnitzler J, Kissling WD, Mosbrugger V, Rijsdijk KF, Seijmonsbergen AC, Versteegh H & Favre A (2019) Origins of global mountain plant biodiversity: Testing the "mountain-geobiodiversity hypothesis'. *Journal of Biogeography* 46: 2826–2838. https://doi.org/10.1111/jbi.13715

Najwer A, Borysiak J, Gudowicz J, Mazurek M & Zwoliński Z (2016) Geodiversity and biodiversity of the postglacial landscape (Dębica River catchment, Poland). *Quaestiones Geographicae* 35: 5–28. https://doi.org/10.1515/quageo-2016-0001

Nichols WF, Killingbeck KT & August PV (1998) The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conservation Biology* 12: 371–379. https://doi.org/10.1111/j.1523-1739.1998.96237.x

National Land Survey of Finland (2012) *Topographic Database*. https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/datasets-and-interfaces/product-descriptions/topographic-database

National Land Survey of Finland (2024a) *Elevation model 2 m*. https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/datasets-and-interfaces/product-descriptions/elevation-model-2-m

National Land Survey of Finland (2024b) *Hillshade (elevation model)*. https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/datasets-and-interfaces/product-descriptions/hillshade

Noss RF (1990) Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology* 4: 355–364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x

Norder SJ (2019) Alexander von Humboldt (1769–1859): Connecting geodiversity, biodiversity and society. *Journal of Biogeography* 46: 1627–1630. https://doi.org/10.1111/jbi.13500

Parks KE & Mulligan M (2010) On the relationship between a resource based measure of geodiversity and broad scale biodiversity patterns. *Biodiversity and Conservation* 19: 2751–2766. https://doi.org/10.1007/s10531-010-9876-z

Pellitero R, Manosso FC & Serrano E (2015) Mid□ and large□ scale geodiversity calculation in Fuentes Carrionas (NW Spain) and Serra do Cadeado (Paraná, Brazil): Methodology and application for land management. *Geografiska Annaler: Series A, Physical Geography* 97(2): 219–235. https://doi.org/10.1111/geoa.12057

Pereira DI, Pereira P, Brilha J & Santos L (2013) Geodiversity assessment of Paraná State (Brazil): An innovative approach. *Environmental Management* 52: 541–552. https://doi.org/10.1007/s00267-013-0100-2

Perotti L, Carraro G, Giardino M, De Luca DA & Lasagna M (2019) Geodiversity evaluation and water resources in the Sesia Val Grande UNESCO Geopark (Italy). *Water* 11(10): 2102. https://doi.org/10.3390/w11102102

Pirinen P, Simola H, Aalto J, Kaukoranta J-P, Karlsson P & Ruuhela R (2012) Climatological statistics of Finland 1981–2010. *Finnish Meteorological Institution Reports* 1: 1–96. http://hdl.handle.net/10138/35880

Poggio L, Sousa LM, Batjes NH, Heuvelink GBM, Kempen B, Ribeiro E & Rossiter D (2021) SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. *SOIL* 7: 217–240. https://doi.org/10.5194/soil-7-217-2021

Polman EMN, Seijmonsbergen AC, Versteegh H & Kissling WD (2024) Global geodiversity components are not equally represented in UNESCO GlobalGeoparks. *Philosophical Transactions of the Royal Society A* 382: 20230054. https://doi.org/10.1098/rsta.2023.0054

Prosser CD, Burek CV, Evans DH, Gordon JE, Kirkbride VB, Rennie AF & Walmsley CA (2010) Conserving geodiversity sites in a changing climate: Management challenges and responses. *Geoheritage* 2: 123–136. https://doi.org/10.1007/s12371-010-0016-7

Raven PJ, Holmes NT, Dawson FH & Everard M (1998) Quality assessment using River Habitat Survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems 8*: 477–499. https://doi.org/10.1002/(SICI)1099-0755(199807/08)8:4<477::AID-AQC299>3.0.CO;2-K

Read QD, Zarnetske PL, Record S, Dahlin KM, Costanza JK, Finley AO, Gaddis KD, Grady JM, Hobi ML, Latimer AM, Malone SL, Ollinger SV, Pau S & Wilson AM (2020) Beyond counts and averages: Relating geodiversity to dimensions of biodiversity. *Global Ecology and Biogeography 29*: 696–710. https://doi.org/10.1111/geb.13061

Ren Y, Lü Y, Hu J & Yin L (2021) Geodiversity underpins biodiversity but the relations can be complex: Implications from two biodiversity proxies. *Global Ecology and Conservation 31*: e01830. https://doi.org/10.1016/j.gecco.2021.e01830

Reynard E & Coratza P (2007) Geomorphosites and geodiversity: A new domain of research. *Geographica Helvetica 62*: 138–139. https://gh.copernicus.org/articles/62/138/2007/gh-62-138-2007.pdf

Ridgeway G & with contributions from others (2017) *gbm: Generalized boosted regression models*. R package version 2.1.3. https://CRAN.Rproject.org/package=gbm

Riihimäki H, Kemppinen J, Kopecký M & Luoto M (2021) Topographic Wetness Index as a proxy for soil moisture: The importance of flow-routing algorithm and grid resolution. *Water Resources Research 57*: e2021WR029871. https://doi.org/10.1029/2021WR029871

Riley SJ, DeGloria SD & Elliot R (1999) A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences 5*(1–4): 23–27. https://download.osgeo.org/qgis/doc/reference-docs/Terrain_Ruggedness_Index.pdf

Roswell M, Dushoff J & Winfree R (2021) A conceptual guide to measuring species diversity. *Oikos 130*: 321–338. https://doi.org/10.1111/oik.07202

Ruban D (2010) Quantification of geodiversity and its loss. *Proceedings of the Geologists' Association 121*(3): 326–333. https://doi.org/10.1016/j.pgeola.2010.07.002

Rytkönen A-M, Ahopelto L, Helkimo J, Olin S, Keto A, Leinonen A & Häggblom O (2024) Valuma-aluesuunnittelun tiekartta vuoteen 2030. *Valtioneuvoston julkaisuja 2024(6)*. http://urn.fi/URN:ISBN:978-952-383-727-0

Räsänen A, Kuitunen M, Hjort J, Vaso A, Kuitunen T & Lensu A (2016) The role of landscape, topography, and geodiversity in explaining vascular plant species richness in a fragmented landscape. *Boreal Environment Research 21*: 53–70. http://hdl.handle.net/10138/225285

Rääpysjärvi J, Hämäläinen H & Aroviita J (2016) Macrophytes in boreal streams: Characterizing and predicting native occurrence and abundance to assess human impact. *Ecological Indicators 64*: 309–318. https://doi.org/10.1016/j.ecolind.2016.01.014

Salminen H, Tukiainen H, Alahuhta J, Hjort J, Huusko K, Grytnes J-A, Pacheco-Riaño LC, Kapfer J, Virtanen R & Maliniemi T (2023) Assessing the relation between geodiversity and species richness in mountain heaths and tundra landscapes. *Landscape Ecology 38*(8): 2227–2240. https://doi.org/10.1007/s10980-023-01702-1

Santucci VL (2005) Historical perspectives on biodiversity and geodiversity. *Geodiversity & Geoconservation 22*(39): 29–34. http://www.georgewright.org/223santucci.pdf

Sayama K (2024) Promoting diversity in geoheritage evaluation: Creating an evaluation method for the scientific value of Quaternary sites in arid environments. *Philosophical Transactions of the Royal Society A 382*: 20230138. https://doi.org/10.1098/rsta.2023.0138

Scammacca O, Bétard F, Montagne D, Rivera L, Biancat C, Aertgeerts G & Heuret A (2024) From geodiversity to geofunctionality: Quantifying geodiversity-based ecosystem services for landscape planning in French Guiana. *Geoheritage 16*(3). https://doi.org/10.1007/s12371-023-00910-0

Schrodt F, Santos MJ, Bailey JJ & Field R (2019) Challenges and opportunities for biogeography—What can we still learn from von Humboldt? *Journal of Biogeography 46*: 1631–1642. https://doi.org/10.1111/jbi.13616

Schrodt F, Vernham G, Bailey J, Field R, Gordon JE, Gray M, Hjort J, Hoorn C, Hunter Jr ML, Larwood J, Lausch A, Monge-Ganuzas M, Miller S, van Ree D, Seijmonsbergen AC, Zarnetske PL & Kissling WD (2024) The status and future of essential geodiversity variables. *Philosophical Transactions of the Royal Society A 382*: 20230052. https://doi.org/10.1098/rsta.2023.0052

Schulze ED, Beck E, Buchmann N, Clemens S, Müller-Hohenstein K & Scherer-Lorenzen M (2019) Interactions between plants, plant communities and the abiotic and biotic environment. In *Plant Ecology*, 689–741. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-56233-8_19

Semeniuk V (1997) The linkage between biodiversity and geodiversity. *In* Eberhard R (ed.) *Pattern and Process: Towards a Regional Approach to National Estate Assessment of Geodiversity*, 51–58. Technical Series No. 2. Australian Heritage Commission & Environment Forest Taskforce, Environment Australia, Canberra.

Seijmonsbergen AC, Guldenaar J & Rijsdijk KF (2018) Exploring Hawaiian long-term insular geodiversity dynamics. *Landform Analysis 35*: 31–43. https://doi.org/10.12657/landfana.035.007

Serrano E & Ruiz-Flaño P (2007) Geodiversity: A theoretical and applied concept. *Geographica Helvetica 62*: 140–147. https://doi.org/10.5194/gh-62-140-2007

Simensen T, Horvath P, Vollering J, Erikstad L, Halvorsen R & Bryn A (2020) Composite landscape predictors improve distribution models of ecosystem types. *Diversity and Distributions 26*(8): 928–943. https://doi.org/10.1111/ddi.13060

Simensen T, Erikstad L & Halvorsen R (2021) Diversity and distribution of landscape types in Norway. *Norsk Geografisk Tidsskrift - Norwegian Journal of Geography 75*(2): 79–100. https://doi.org/10.1080/00291951.2021.1892177

Simensen T, Halvorsen R & Erikstad L (2022) Gradient analysis of landscape variation in Norway. *Sommerfeltia 40*: 1–193. https://doi.org/10.2478/som-2022-0001

Soininen J, Bartels P, Heino J, Luoto M & Hillebrand H (2015) Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience 65*(2): 174–182. https://doi.org/10.1093/biosci/biu216

Sørensen R, Zinko U & Seibert J (2006) On the calculation of the topographic wetness index: Evaluation of different methods based on field observations. *Hydrology and Earth System Sciences 10*: 101–112. https://doi.org/10.5194/hess-10-101-2006

Stein A, Gerstner K & Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters 17*: 866–880. https://doi.org/10.1111/ele.12277

Stanley M (2004) Geodiversity - Linking people, landscapes and their culture. https://www.researchgate.net/publication/285890010_Geodiversity_-_linking_people_landscapes_and_their_culture (accessed 15 May 2024)

Strahler AH (2013) *Introducing physical geography*. 6th edition. Wiley.

Stefanidis K, Karaouzas I, Oikonomou A, Smeti E, Kouvarda T, Latsiou A, Vourka A & Dimitriou E (2023) Geodiversity as a potential indicator of stream health in ecological quality assessment systems. *Ecohydrology 16*(6): e2551. https://doi.org/10.1002/eco.2551

Thomas MF (2012) Geodiversity and landscape sensitivity: A geomorphological perspective. *Scottish Geographical Journal* 128(3–4): 195–210. https://doi.org/10.1080/14702541.2012.725863

Toivanen M, Hjort J, Heino J, Tukiainen H, Aroviita J & Alahuhta J (2019) Is catchment geodiversity a useful surrogate of aquatic plant species richness? *Journal of Biogeography* 46: 1711–1722. https://doi.org/10.1111/jbi.13648

Toivanen M, Maliniemi T, Hjort J, Salminen H, Ala-Hulkko T, Kemppinen J, Karjalainen O, Poturalska A, Kiilunen P, Snåre H, Leppiniemi O, Makopoulou E, Alahuhta J & Tukiainen H (2024a) Geodiversity data for Europe. *Philosophical Transactions of the Royal Society A* 20230173. https://dx.doi.org/10.1098/rsta.2023.0173

Toivanen M, Maliniemi T, Hjort J, Salminen H, Ala-Hulkko T, Kemppinen J, Karjalainen O, Poturalska A, Kiilunen P, Snåre H, Leppiniemi O, Makopoulou E, Alahuhta J & Tukiainen H (2024b) Geodiversity data for Europe at 1-km and 10-km resolutions [Data set]. *Dryad.* https://doi.org/10.5061/dryad.crjdfn39c

Toivonen H & Huttunen P (1995) Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquatic Botany* 51: 197–221. https://doi.org/10.1016/0304-3770(95)00458-C

Tukiainen H, Alahuhta J, Field R, Ala-Hulkko T, Lampinen R & Hjort J (2017a) Spatial relationship between biodiversity and geodiversity across a gradient of land-use intensity in high-latitude landscapes. *Landscape Ecology* 32: 1049–1063. https://doi.org/10.1007/s10980-017-0508-9

Tukiainen H, Bailey JJ, Field R, Kangas K & Hjort J (2017b) Combining geodiversity with climate and topography to account for threatened species richness. *Conservation Biology* 31: 364–375. https://doi.org/10.1111/cobi.12799

Tukiainen H & Hjort J (2021) Maisematason geodiversiteetti Suomessa. *Terra* 133(2): 55–76. https://doi.org/10.30677/terra.99435 [In Finnish]

Tukiainen H & Bailey JJ (2023) Enhancing global nature conservation by integrating geodiversity in policy and practice. *Conservation Biology* 37: e14024. https://doi.org/10.1111/cobi.14024

Tukiainen H, Maliniemi T, Alahuhta J, Hjort J, Lindholm M, Salminen H, Snåre H, Toivanen M, Vilmi A & Heino J (2023) Quantifying alpha, beta and gamma geodiversity. *Progress in Physical Geography: Earth and Environment* 47(1): 140–151. https://doi.org/10.1177/03091333221114714

Tukiainen H, Toivanen M & Maliniemi T (2023) Geodiversity and biodiversity. *Geological Society, London, Special Publications* 530: 31–47. https://doi.org/10.1144/SP530-2022-107

Tukiainen H, Maliniemi T, Brilha J, Alahuhta J & Hjort J (2024) A framework for quantifying geodiversity at the local scale: A case study from the Rokua UNESCO Global Geopark. *Philosophical Transactions of the Royal Society A* 382: 20230059. https://doi.org/10.1098/rsta.2023.0059

Tukiainen H, Bailey JJ & Hjort J (manuscript) Geodiversity and biodiversity linkages in theory and practice for nature conservation. In Reynard E & Brilha J (eds.) *Geoheritage: Assessment, Protection and Management.* (2nd Ed.). Elsevier. *In review.*

Turner MG (1989) Landscape ecology: The effect of pattern on process. *Annual Review of Ecology, Evolution, and Systematics* 20(1): 171–197. https://doi.org/10.1146/annurev.es.20.110189.001131

Underwood E, Taylor K & Tucker G (2018) The use of biodiversity data in spatial planning and impact assessment in Europe. *Research Ideas and Outcomes* 4: e28045. https://doi.org/10.3897/rio.4.e28045

UNESCO (2022) *Records of the General Conference 41st session*, Paris, 9–24 November 2021, Volume 1 Resolutions. https://unesdoc.unesco.org/ark:/48223/pf0000380399

UNESCO (2023) *Seven reasons why "Geodiversity is for everyone"*. 5 October 2023. https://www.unesco.org/en/articles/seven-reasons-why-geodiversity-everyone (accessed 15 May 2024)

USDA, United States Department of Agriculture (1999) *Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys*. 2nd Edition. Natural Resources Conservation Service. Agriculture Handbook 436. USDA. https://www.nrcs.usda.gov/sites/default/files/2022-06/Soil%20Taxonomy.pdf

USDA, United States Department of Agriculture (2017) *Soil survey manual.* Handbook 18. USDA. https://www.nrcs.usda.gov/sites/default/files/2022-09/The-Soil-Survey-Manual.pdf

van Ree CCDF, van Beukering PJH & Boekestijn J (2017) Geosystem services: A hidden link in ecosystem management. *Ecosystem Services* 26(A): 58–69. https://doi.org/10.1016/j.ecoser.2017.05.013

van Ree D, van Beukering PJH & Hofkes MW (2024) Linking geodiversity and geosystem services to human well-being for the sustainable utilization of the subsurface and the urban environment. *Philosophical Transactions of the Royal Society A* 382: 20230051. https://doi.org/10.1098/rsta.2023.0051

Vernham G, Bailey JJ, Chase JM, Hjort J, Field R & Schrodt F (2023) Understanding trait diversity: The role of geodiversity. *Trends in Ecology and Evolution* 38(8): P736–P748. https://doi.org/10.1016/j.tree.2023.02.010

Viles H & Coombes M (2022) Biogeomorphology in the Anthropocene: A hierarchical, traits-based approach. *Geomorphology* 417: 108446. https://doi.org/10.1016/j.geomorph.2022.108446

Viles HA, Naylor LA, Carter NEA & Chaput D (2008) Biogeomorphological disturbance regimes: Progress in linking ecological and geomorphological systems. *Earth Surface Processes and Landforms* 33: 1419–1435. https://doi.org/10.1002/esp.1717

Virtanen R, Luoto M, Rämä T, Mikkola K, Hjort J, Grytnes JA & Birks HJB (2010) Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography* 19: 810–821. https://doi.org/10.1111/j.1466-8238.2010.00570.x

Wallis CIB, Tiede YC, Beck E, Böhning-Gaese K, Brandl R, Donoso DA, Espinosa CI, Fries A, Homeier J, Inclan D, Leuschner C, Maraun M, Mikolajewski K, Neuschulz EL, Scheu S, Schleuning M, Suárez JP, Tinoco BA, Farwig N & Bendix J (2021) Biodiversity and ecosystem functions depend on environmental conditions and resources rather than the geodiversity of a tropical biodiversity hotspot. *Scientific Reports* 11: 24530. https://doi.org/10.1038/s41598-021-03488-1

Ward JV, Tockner K, Arscott DB & Claret C (2002) Riverine landscape diversity. *Freshwater Biology* 47: 517–539. https://doi.org/10.1046/j.1365-2427.2002.00893.x

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338. https://doi.org/10.2307/1943563

Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21: 213–251. https://doi.org/10.2307/1218190

Wolniewicz P (2023) Quantifying geodiversity at the continental scale: Limitations and prospects. *Resources* 12(5): 59. https://doi.org/10.3390/resources12050059

Wong DW (2009) Modifiable areal unit problem. *International Encyclopedia of Human Geography* 2009: 169–174. https://doi.org/10.1016/B978-008044910-4.00475-2

Wu J (2004) Effects of changing scale on landscape pattern analysis: Scaling relations. *Landscape Ecology* 19: 125–138. https://doi.org/10.1023/B:LAND.0000021711.40074.ae

Wu J (2006) Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology* 21: 1–4. https://doi.org/10.1007/s10980-006-7195-2

Wu J (2013) Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. *Landscape Ecology* 28: 1–11. https://doi.org/10.1007/s10980-012-9836-y

Wüest RO, Zimmermann NE, Zurell D, Alexander JM, Fritz SA, Hof C, Kreft H, Normand S, Cabral JS, Szekely E, Thuiller W, Wikelski M, Karger DN (2020) Macroecology in the age of Big Data – Where to go from here? *Journal of Biogeography* 47: 1–12. https://doi.org/10.1111/jbi.13633

Yamazaki D, Trigg MA & Ikeshima D (2015) Development of a global ~90 m water body map using multi-temporal Landsat images. *Remote Sensing of Environment* 171: 337–351. https://doi.org/10.1016/j.rse.2015.10.014

Zarnetske PL, Read QD, Record S, Gaddis KD, Pau S, Hobi ML, Malone SL, Costanza J, Dahlin KM, Latimer AM, Wilson AM, Grady JM, Ollinger SV & Finley AO (2019) Towards connecting biodiversity and geodiversity across scales with satellite remote sensing. *Global Ecology and Biogeography* 28: 548–556. https://doi.org/10.1111/geb.12887

Zhu G, Giam X, Armsworth PR, Cho SH & Papeš M (2023) Biodiversity conservation adaptation to climate change: Protecting the actors or the stage. *Ecological Applications* 33(2): e2765. https://doi.org/10.1002/eap.2765

Zwoliński Z, Najwer A & Giardino M (2018) Methods for assessing geodiversity. In Reynar E & Brilha J (eds.) *Geoheritage: Assessment, Protection, and Management*, 27–52. https://doi.org/10.1016/B978-0-12-809531-7.00002-2