Advancing biodiversity and species distribution modelling using geodiversity information

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"We need a more holistic approach to valuing, conserving and managing nature that includes both geodiversity and biodiversity and this is particularly true at a time when the threats to nature are increasing from human actions and climate change. If we do not do so, we simply undervalue nature."

Murray Gray, 2012

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EXTENDED THESIS ABSTRACT

Context

Understanding spatial patterns of biodiversity and species' distributions is important for scientific theory, and for conservation and management of the natural world. Climatic variables are widely recognised as strong correlates of species richness over large spatial extents. Correlates of species richness at smaller extents (regional and landscape scales) are less well established, but environmental heterogeneity is widely thought to be important. A large number of environmental heterogeneity measures have been used, but in particular there is a growing interest in 'geodiversity', which I define here as the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms. Recent research has emphasised both geodiversity's inherent value and its potential as a correlate and predictor of spatial biodiversity and species' distribution patterns. However, despite this clear potential of geodiversity for improving our understanding of how patterns of life relate to environmental heterogeneity, its incorporation into biodiversity and species' distribution modelling is substantially underdeveloped. In this thesis, using a macroecological approach I begin to address some of these knowledge gaps by analysing the relationships between geodiversity data, and its constituent 'geofeatures', and species richness and distributions for multiple taxa and across several scales (grain size and extent) and geographic locations. My main aims in this thesis are to more fully evaluate geodiversity itself, and improve our understanding of its role with respect to the spatial patterning of biodiversity, both conceptually and empirically.

Locations and Spatial Scales

Analyses were carried out within and across Great Britain (England, Scotland, and Wales) and Finland. The order of the four quantitative papers generally reflects the largest spatial extent (i.e. size of the study area) at which they were conducted, from national (PAPERS II and III) through landscape (PAPER IV), to the local scale (vegetation plots within a small upland river catchment; PAPER V). PAPER II is a study across several spatial extents (from landscape to national) and uses two grain sizes (1 km^2 and 100 km^2). PAPER I is a review paper that considers multiple scales and geographic locations conceptually.

Time period

Present day: data were from between 1995 and 2016 across all of the quantitative studies.

Taxa

Multiple: alien and native vascular plants across Great Britain (PAPER II); threatened bryophytes, beetles, fungi, lepidoptera, lichens, mammals, molluscs, and vascular plants across Finland (PAPER III); common and rare vascular plants across the Cairngorms, Scotland (PAPER IV); angiosperms, conifers, fungi, lichens, liverworts, lycophytes, mosses, and pteridophytes (and productivity) across an upland river catchment within the Cairngorms (PAPER V); and conceptual consideration of multiple taxa (PAPER I).

Methods

For studies in Great Britain, plant data were provided by the Botanical Society of Britain and Ireland (BSBI) for PAPERS II and IV, and by the Centre for Ecology and Hydrology (CEH) for PAPER V. The threatened species data in Finland were from Finnish Environment Institute (PAPER II). Species richness (PAPERS II, III, and IV), rarity-weighted richness (RWR; PAPER III), species' distributions (PAPERS IV and V), and productivity (measured using NDVI from colour infrared aerial imagery; PAPER V) were all analysed using Boosted Regression Tree (BRT) modelling, allowing comparisons between studies.

For geodiversity data in the British studies, I compiled geodiversity data on landforms, soils, hydrological and geological features using existing national datasets (e.g. British Geological Survey), and used a geomorphometric method to extract landform coverage data (landforms included: hollows, ridges, valleys, and peaks). These data were analysed alongside environmental data, which varied between papers, relating to climate, standard topography (e.g. slope; elevation), land use, and human population. The sources of other geodiversity data in Finland, and environmental data on topography and climate, came from a variety of sources, which are detailed within each paper.

Results

Geodiversity improved biodiversity and species' distribution models throughout all of the quantitative analyses and generally declined in importance as spatial scale coarsened beyond the landscape scale. At most spatial scales and in most places, the roles of climate and/or coarse

topography dominated, and geodiversity played a relatively small role, as was expected. Geodiversity, however, made consistent positive contributions to the models independently of traditionally used topographic metrics such as standard deviation of elevation and slope. Taxonomically, geodiversity: (i) was slightly more relevant for native vascular plants than alien in Great Britain (PAPER II); (ii) of similar relevance to common and rare vascular plants in the Scottish Highlands, except that the coverage of soil parent material was especially important for rare species' distributions (PAPER IV); of similar relevance to most sessile taxa (angiosperms, fungi, mosses, liverworts, lichens, pteridophytes, and lycophytes; conifers were not related to geodiversity) in an upland Scottish river catchment (PAPER V); and more important for threatened vascular plants and bryophytes over other studied taxa in Finland (PAPER II). Geodiversity also improved models of productivity, and the variability in productivity, in PAPER V.

Main conclusions and Future Directions

Geodiversity improves our understanding of, and ability to model, the relationship between biodiversity and environmental heterogeneity at multiple spatial scales, by allowing us to get closer to the real-world conditions and processes that affect life. I found that the greatest benefit comes from measuring 'geofeatures', which describe the constituent parts of geodiversity separately, rather than as one combined variable. Automatically extracted landform data, the use of which is novel in ecology, biogeography and macroecology, proved particularly valuable throughout this body of work, and as too did data from expert geological and hydrological maps.

The idea of 'Conserving Nature's Stage' (CNS), and identifying areas that are most capable of supporting high biodiversity into the future, the benefits and caveats of which are discussed in this thesis, has recently emerged. It requires a sound empirical and conceptual basis, to which my research contributes. In this thesis, I have gone some way towards demonstrating the conceptual and empirical value of incorporating geodiversity into ecological analyses across multiple spatial scales, paving the way for this recent approach to be more extensively used for theoretical and applied purposes. I accomplished this by carrying out an assessment of existing geodiversity literature and, importantly, looking forwards to consider the prospects of geodiversity within ecology (PAPER I), supported by four quantitative studies. The conservation significance is emphasised in PAPER III.

Much remains to be done, however, and future research directions are detailed in PAPER I. We need to develop predictive models to test the role of geodiversity across an array of

geographical and taxonomic domains, as well as to assess metrics beyond species richness and species' distributions. One example may involve beta diversity: does spatial turnover in species relate to spatial turnover in geofeatures? Fully analysing the role of geodiversity through time will also be important, including in relation to refugia, given predicted environmental changes in climate. In progressing with this line of enquiry, we will improve our knowledge and understanding of patterns of life on Earth and, specifically, how the geophysical landscape helps shape them.

A MEMORANDUM ON THE PAPERS

Each of the papers, which are at various stages of publication as outlined on the next page, is included herein as follows: (i) the author's accepted manuscript (AAM) is presented below if the paper has been published; or (ii) the most recent version is presented where the manuscript is in the final stage of preparation but not yet submitted. For (i), there may be minor discrepancies between the AAM and the published version resulting from the copy-editing process.

Where possible, Supporting Information (SI) is provided for each paper under the relevant sections at the end of the thesis. All SI is also available online, including purely digital resources and PDFs of the published papers (II and III). Online SI can be accessed at: https://www.dropbox.com/s/r81j86asojcyt3q/JJB_2017_PhD_SI.zip (password: cGZdzP6Ze8).

Author contributions are included towards the end of each paper and also appear in the published versions, where applicable. I was the lead author on all papers, except PAPER III, where Helena Tukiainen and I were joint first author, each making an equal contribution, as noted on the front page of the published paper.

PAPER I will shortly be submitted as a review paper and focuses heavily on the prospects of geodiversity in ecology, after providing a full literature review. Chronologically, though not in the thesis, this paper is positioned after PAPERS II and III and the 'prospect' section of PAPER I outlines the potential of geodiversity going forwards, given that these papers are already published, and should be read as such. PAPERS II and III are themselves referenced throughout PAPER I and elsewhere as 'Bailey et al. (2017)' and 'Tukiainen, Bailey, et al. (2017)', respectively (or, for the latter in PAPERS IV and V, as 'Tukiainen et al. (2017)'). References to the as-yet unpublished quantitative papers (IV and V) are also included in PAPER I.

References, tables, and figures are all self-contained within each paper. Styles may vary according to the journal/target journal.

The current status of each paper is described on the next page.

The current status of each paper

Paper № in Thesis	Title	Status (Date accepted)	Journal or (Target Journal)	Page № in Thesis
I	Geodiversity, Ecological Mechanisms, and Scale: Assessment and Prospect.	Co-authors' final edits in progress	(*Biological Reviews*)	p. 15
II	Modelling native and alien vascular plant species richness: at which scales is geodiversity most relevant? Linked DOI: 10.1111/geb.12574.	Published (2017)	*Global Ecology and Biogeography*	p. 65
III	Combining geodiversity with climate and topography to account for threatened species richness. Linked DOI: 10.1111/cobi.12799.	Published (2017)	*Conservation Biology*	p. 93
IV	Modelling common and rare plant diversity and distributions in relation to geodiversity in an upland landscape.	Co-authors' final edits in progress	*(Landscape Ecology)*	p. 115
V	Relating geodiversity to species' distributions and cross-scale productivity in an upland river catchment.	Co-authors' final edits in progress	(*Plant Ecology and Diversity*)	p. 141

PAPER I: GEODIVERSITY, BIODIVERSITY, AND SCALE: ASSESSMENT AND PROSPECT

Bailey, Joseph J. * [1], Bouten, W. [2], Boyd, D.S. [1], Field, R. [1], Flantua, S.G.A. [2], Kissling, W.D. [2], Schrodt, F. [1], Seijmonsbergen, A.C. [2], van Loon, E. [2], Rijsdijk, K. [2]

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Status as a paper: Co-authors' final edits in progress

Abstract

Consider two landscapes with a similar mean and standard deviation in elevation, aspect, and slope, but where one has greater landform and geological variety: the latter, given a similar climate, would likely host more species because of the greater variety of abiotic conditions and associated increased resource gradients and niche space. In other words, the *geodiversity* in the second landscape produces greater biodiversity. Geodiversity is the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms. Geodiversity and its constituent geofeatures have proved useful explanatory variables in ecological studies across a range of spatial scales and have been used towards conservation efforts (Conserving Nature's Stage). However, geodiversity still lacks full conceptual integration with ecological theory, which is needed for a better understanding of species' distributions and diversity now and for predicting how these might change into the future.

We therefore provide herein an overarching assessment of geodiversity research to date. Importantly, this is through the *eye of an ecologist*, rather than an earth scientist, which is where geodiversity as a concept was born. In doing so, we aim to integrate this relatively new concept within existing ecological theory and frameworks, more extensively than any previous work. In particular, we describe ecologically relevant abiotic processes and conditions that result from geodiversity and geofeatures. After assessing the current state of geodiversity research, we consider the prospects going forwards within conservation, ecology, and biogeography, with comments on data availability and the relevance of geodiversity in the context of climate change. We highlight the need for a fuller appreciation of spatial and temporal scale in geodiversity work to date and, as a response to this, develop a cross-scale spatio-temporal conceptual framework in accordance with the existing biogeography literature. Our assessment and framework should allow ecologists to more easily understand and appreciate the relevant ecological mechanisms and physical conditions and processes that we are trying to capture with geodiversity.

Introduction

Spatial patterns of life develop through time as a result of the interactions between living organisms and the surface of the Earth. The Earth's surface itself is diverse in space and changes through time, and this affects the diversity of life. This environmental heterogeneity across the Earth's surface has been associated with higher levels of biodiversity (Stein et al. 2014). In this context, however, environmental heterogeneity has generally been

quantitatively and analytically limited to relatively crude topographic parameters (e.g. mean and range in elevation and slope; ruggedness; openness). Recent research has begun to explore and demonstrate the value of measuring explicit land surface features (geofeatures: landforms, streams, geology), which comprise 'geodiversity', for modelling biodiversity at a range of scales (Bailey et al. 2017; Hjort et al. 2012; Anderson et al. 2015). Specifically, geodiversity adds explanatory power above and beyond the 'traditional', crude topographic metrics (Bailey et al. 2017). The use of these data in conservation has also been demonstrated as part of as part of the Conserving Nature's Stage approach (Beier et al. 2015).

Given these demonstrated links between the geophysical environment and patterns of life, it follows that studies of biodiversity and species' distributions are likely to benefit from the incorporation of explicit abiotic environmental features (geofeatures) and their diversity (geodiversity). These data may be especially relevant at smaller spatial extents where broad climatic and topographic conditions are relatively uniform (Willis & Whittaker 2002; Whittaker et al. 2001; Hawkins et al. 2003). We exist in a time when it is possible to measure advanced heterogeneity variables at finer spatial and temporal scales than previously possible, including habitat-related heterogeneity metrics derived from remote sensing (e.g. Tuanmu & Jetz 2015). Abiotic and habitat heterogeneity metrics are needed to advance our understanding of patterns of life. Here, we review and conceptually clarify and advance a category of environmental heterogeneity variables relating to 'geodiversity', which have recently shown great potential in ecology and conservation. However, these data lack conceptual integration. We also discuss scale in detail and identify the limits of geodiversity in space and time, based on existing frameworks.

Assessment: Geodiversity in Ecology

Defining geodiversity for use in ecology

The semantic origin of 'geodiversity' is not straightforward. However, it seems to have essentially been born out of geology as a synonym for 'abiotic diversity', where the concept was developed before its value in biodiversity science and ecology was realised (Gray 2013; Serrano et al. 2009). This means that work incorporating geodiversity into biodiversity science, spatial ecology, and macroecology has tended to lack definitive links to ecological theory, mechanisms, and processes. In ecology, geodiversity has been mainly discussed in the conservation literature, chiefly around the concept of *Conserving Nature's Stage* (Anderson & Ferree 2010; Theobald et al. 2015). For example, a 2015 special issue of *Conservation Biology* reviewed geodiversity in the context of biodiversity conservation and progressed work on the

incorporation of ecological theory into geodiversity research (Lawler et al. 2015). This issue identified the potential of geodiversity in studies on climate resilience and refugia (Gill et al. 2015) and the need for abiotic surrogates in coarse-filter conservation planning (Beier et al. 2015). Elsewhere, the value of integrating the conservation of biodiversity and geodiversity, with a focus on the European Union, has been discussed in detail (Matthews 2014) and others have striven to create 'ecologically-relevant maps' for conservation planning and climate adaptation from landforms and physiographic diversity (Theobald et al. 2015).

The quantification of geodiversity will always at least partly depend on the purpose of the research or project and the data available. The geodiversity of an area might be of interest from a purely geomorphological or geological point of view (Hjort & Luoto 2010; Pereira et al. 2013), for its geoheritage or geoconservation value (De Wever et al. 2015; Coratza et al. 2015; Henriques & Pena dos Reis 2015; Peña et al. 2016), geosystem service provision (Gray et al. 2013; Hjort et al. 2015), or for its links to biodiversity (Hjort et al. 2012; Tukiainen, Bailey, et al. 2017; Bailey et al. 2017).

Similarly to biodiversity, geodiversity has been quantified using both simple and more complex measures (Table 1). One frequently used geodiversity metric is a basic count of the number of geofeatures, sometimes across multiple geofeature categories, such as hydrology, geology, and geomorphological landforms (Hjort & Luoto 2010; e.g. Serrano & Ruiz-Flaño 2007; Melelli 2014; Pellitero et al. 2010; Athanasios et al. 2016; Pereira et al. 2013). These feature counts per geodiversity category have been used for a number of applications, such as mapping (Melelli 2014), or as factors within biodiversity modelling (Tukiainen, Bailey, et al. 2017; Hjort et al. 2012; Tukiainen, Alahuhta, et al. 2017). More complex measures include terrain ruggedness (e.g. Serrano et al. 2009; Stepišnik & Trenchovska 2017) and extensive landform and land facet diversity mapping used, for example, to identify sites that are sensitive in a geoconservation and land management context (Bradbury 2014; Peña et al. 2016), and with climate resilience and adaptation in mind (Theobald et al. 2015; Albano 2015; Anderson et al. 2014). Our ability to create these metrics and quantify geodiversity has only recently developed: novel datasets offering consistent coverage across large areas combined with equally novel computational tools means that we can quantify landscapes like never before.

Table 1 Selected geodiversity metrics used in recently research and, where applicable, the result when used to model biodiversity.

Metric class	Geodiversity quantification / formula	Selected examples	Notes and: if biodiversity was also considered, what was the result (if not = NA)? (country)
Related to geofeature richness	$G = \frac{N * R}{lnS}$ Where: G = geodiversity; N = number of geofeatures; R = roughness; S = surface area of site	Serrano et al. (2009)	NA (Spain)
		Hjort and Luoto (2010)	NA (Finland)
		Pellitero et al. (2010)	NA (Spain)
	Diversity (richness) of geofeatures assessed individually	Hjort et al. (2012)	Plant species richness models' predictive ability and explanatory power increased. (Finland)
		Pereira et al. (2013)	NA
		Tukiainen et al. (2017a)	Geodiversity was most relevant in areas of moderate to high human impact. (Finland)
		Tukiainen et al. (2017b)	Geodiversity metrics improved models of rarity-weighted richness (RWR). (Finland)
		Bailey et al. (2017)	Highly limited model contributions of land surface material richness compared to landform coverage data (below). (Great Britain)
Coverage of geofeatures	Landforms' and hydrological features' size modelled individually (GDCs)	Bailey et al. (2017)	Improved models of native and alien plant richness, especially at landscape scales. (Great Britain)
Shannon Diversity Index (*H*) (or related to)	$H = -\sum_{i=1}^{S}(p_i \ln p_i)$ Where: S = geofeature richness; p_i = proportion of S made up of the ith geofeature	Albano (2015)	NA (USA)
		Theobald et al. (2015)	(Normalised Shannon Diversity Index to produce Shannon's equitability). Physiographic diversity correlated reasonably well with vertebrate species richness (0.449). (USA)
Multiple indices	Richness; Shannon and Simpson diversity and evenness	Athanasios et al. (2016)	NA (Greece)

While various measures of geodiversity exist, for a number of purposes, there is no consensus regarding the conceptual limits of geodiversity. For example, a relatively broad designation considers geodiversity simply as "the diversity of the geosphere", including "climate, topography, geology and hydrology" (Parks & Mulligan 2010). Such a broad definition including climate seems unhelpful in most ecological studies, with little conceptual advantage to using 'geodiversity' in this way. Others consider geodiversity to include simple topographic variables derived from digital elevation models (DEMs), such as aspect and mean elevation and slope (Mutke & Barthlott 2007; Räsänen et al. 2016). These DEM-derived metrics are useful – depending on scale and geographic location – for models aimed at understanding patterns of life, but separating explicit geofeatures allows better linkage between quantification and underlying mechanism (Bailey et al. 2017). Further, different facets of environmental heterogeneity may complement, and not compete with, one another because of low multicollinearity (Bailey *et al*., 2017).

For this reason, we use a narrow definition of geodiversity, which we would encourage more generally. Importantly, we use the term 'geofeature' to identify a "spatially explicit landform, hydrological feature, or land surface material that is homogeneous within a limited spatial scale, whilst providing heterogeneity across a larger area, and potentially through time". The combined contribution from geofeatures is a measure of geophysical diversity or 'geodiversity', which we define as "the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms" (after Bailey et al. 2017) (Fig. 1). It relates to the natural range and variability of superficial geological (rocks, minerals, fossils), geomorphological (landforms), hydrological (streams, springs, lakes) and soil (chemical and physical) features (Gray 2013; Seijmonsbergen et al. 2014). Like biodiversity, geodiversity can be quantified and measured as the presence, coverage, and frequency of geofeatures within a region, grid cell, or geo-ecological unit (Serrano & Ruiz-Flaño 2007; Serrano et al. 2009; Pellitero et al. 2010). A quantified geofeature (e.g. the coverage of a type of landform or the length of a stream) may be referred to as a 'geodiversity component' (GDC) (Bailey et al. 2017). The definition that we use aims to conceptually and unambiguously differentiate the use of geodiversity from other measures of abiotic environmental heterogeneity (review by Stein et al. 2014) and from crude topographic variables derived from a digital elevation model (DEM). It is applicable to any terrestrial geographic setting and spatial scale and ensures that the focus is on explicit geofeatures and is not just an all-encompassing synonym for abiotic heterogeneity.

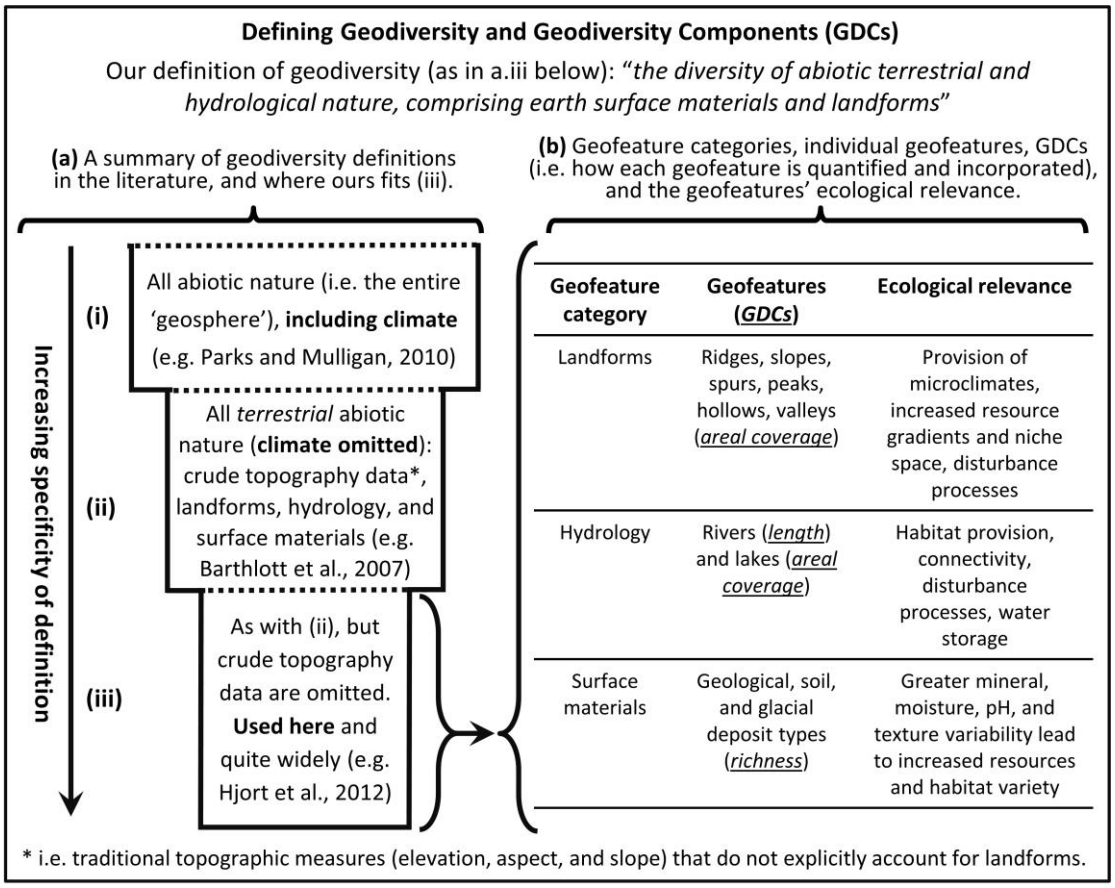


Figure 1 Figure and caption reproduced from Bailey et al. (2017; their Fig. 1). Our definition of 'geodiversity', which is amongst the more specific in the context of the wider literature. It omits relatively crude topography and climate data (a) and consists of geodiversity components (GDCs). The GDCs used in our study, and their associated geofeatures and ecological relevance, are listed (b).

Our detailed definition of geodiversity is aimed at providing a distinct concept that can operate alongside existing facets of environmental heterogeneity. We would also note that, whilst we aim here at providing a comprehensive overview, we do focus on terrestrial environments and a slight adjustment would be required to make this definition applicable to the marine realm, in which only limited geodiversity work has been conducted (Hogg et al. 2016; Sutcliffe et al. 2015). A definition in this domain could be built around "the diversity of sea floor materials and landforms", for example. Our given definition may also need modification for use in coastal environments.

Quantitative studies of geodiversity in ecology to date

Geodiversity has already shown much promise in biodiversity modelling studies. It improved vascular plant biodiversity models for two boreal landscapes (measuring 110 km^2 and 362 km^2) in Finland beyond standard DEM-based topographic data (Hjort et al. 2012). Here, three geodiversity measures were used alongside climatic and topographic (elevation, slope,

wetness) data: geological diversity, geomorphological diversity, and hydrological diversity. The variables' model contributions were assessed separately and in combination. Whilst the identification of ecological mechanisms was limited in this study, it represents a significant progression in the use of geodiversity in biodiversity modelling. The diversity of predicted geomorphology, geology, and hydrology have also been shown to improve models and understanding of threatened species across Finland's national parks for multiple taxa (Tukiainen, Bailey, et al. 2017). Meanwhile, cross-scale geodiversity-biodiversity patterns were highlighted in a macroecological analysis of Great Britain's alien and native vascular plants (Bailey et al. 2017) and, elsewhere, geological diversity has been closely linked to vegetation patterns (Keith 2011; Kougioumoutzis & Tiniakou 2014; Anderson et al. 2015; Anderson & Ferree 2010).

Undoubtedly, much progress has been made. Key and under-considered questions emerge, however, when we wish to incorporate geodiversity into ecology: do these metrics have sufficient ecological meaning; do they capture ecologically-relevant processes; and are they effective for applied purposes in conservation and management? In other words, if we do not know which geofeatures are most important for a given ecological response variable (e.g. species richness) because everything is amalgamated into a single metric, then how helpful can this be? Alternatively, is there more to be gained from studying geofeatures individually, perhaps then combining their model contributions to assess the overall geodiversity contribution? This latter approach has recently proved successful (Bailey et al. 2017), but there is still a need to make explicit links between geofeatures, various aspects of biodiversity, individual species' distributions, and conservation. This progression begins with a better conceptual and theoretical grounding for mechanistic ecological links to geofeatures across scales, which we provide here.

Linking geodiversity to existing ecological theory

The idea that landforms and other geofeatures should relate to ecological patterns is not new (Swanson et al. 1988). However, geodiversity provides a means by which to package a number of novel and existing geophysical parameters, which are currently conceptually disparate. In a general sense, landforms are spatially explicit units within landscapes that affect abiotic conditions, including, but not limited to: air and ground temperature; soil parent material; local aspect and slope; nutrients; pH; soil moisture; humidity. Meanwhile, a geofeature such as a stream offers connectivity and several types of geofeature may contribute towards local geomorphological disturbance events, which then affect local resource gradients and the competitive environment (Virtanen et al. 2010). In short, greater geodiversity theoretically

produces increased resource gradients, which have been widely linked to productivity and biodiversity (Lavers & Field 2006). We have summarised some of these relationships in Table 2 for specific geofeatures, and discuss the broader categories (landforms; land surface materials; hydrology) thereafter.

Table 2 A non-exhaustive assessment of geofeatures and theorised ecological relevance. The brief descriptions aim to capture multiple environmental settings and provide a generalised overview of key factors, conditions, and processes of ecological relevance, but the idiosyncrasies of each geofeature will be heavily influenced by the study site's geographical settings and scale, and focal taxa. Some geofeatures will promote biodiversity, whilst others present harsh environments that may be important for rare or specialist species. Prospect: these geofeatures are placed within our spatio-temporal framework in Figure 2 using a subset of the geofeatures listed here.

Geofeature category	Geofeature (details)	Ecological Relevance
Landforms	Slope	Slope as a geofeature simply relates to knowing that a slope landform is individually present (i.e. it is not part of another landform), and not knowing properties of the slope (gradient and aspect) as can be measured using traditional topographic measures. The presence of a slope can increase or decrease the amount of solar radiation received, depending on its aspect, and can affect moisture levels because of effects of water flow. Higher species richness has been observed on slopes (and ridges) compared to valleys for species that survive well in exposed, windy environments (Kubota et al. 2004). Slopes are also likely to be relevant in relation to disturbance events, which are known to be ecologically important (Le Roux et al. 2013), and control the flow of water in a landscape (Keppel et al. 2015), perhaps more so than other landforms.
	Peak (where more than two upward slopes converge)	Identifying areas with lower species richness unlikely to support species is as important as identifying those higher in species richness. Peaks often provide exposed and harsh environments with relatively high wind speeds, low temperatures, high moisture, and minimal/non-existent top soil, making it difficult for most organisms to establish and persist. Deflation surfaces may be found on and around peaks (Wrightham & Kempe 2006), depending on the environment.
	Pit (sink / depression) (where more than two downward slopes converge)	Pits are likely to be important for moisture, and can even host temporary pools, which may be especially important for rare species (Hjort et al. 2015; Vandvik et al. 2005). Pits can provide a sheltered environment, protecting species from high winds, possibly direct sunlight, and grazing animals, in upland areas. Greater soil depth may also be found in a pit as sediment accumulates over time. The low light and increased moisture will also make it difficult for non-specialist species to establish and, in colder environments, pits may be snow-free for a reduced period unless they are subject to high levels of wind exposure (Löffler 2005). Meanwhile, in water-poor environments small pits in an otherwise flat landscape can be significant, given the 'great ecological value' of water and the ability of these landforms to store it (Kidron 2014).
	Hollow (a depression in a slope)	Hollows are likely to provide a cooler and moister environment than the surrounding slope because they intercept falling sediment and flowing water. The microclimatic conditions mean that snow patches are more likely to persist in hollows compared to surrounding parts of a landscape; the presence of snow can be significant for plants, affecting growth and the timing of flowering

		and fruiting (Harshberger 1929). Areas of a landscape that support late snow have been linked to a lower overall biomass, but greater species richness (Litaor et al. 2008). Hollows may also represent corries, which typically have a cliff-like backwall (Jonasson et al. 2005): see 'Cliff or escarpment' below.
	Spur (a protrusion in a slope where a ridge extends downwards)	Spurs and ridges are comparable landforms in terms of their ecological relevance. All have a crest of some sort, which is typically exposed to wind and lower temperatures. Deflation surfaces may be found on and around ridges (Wrightham & Kempe 2006), depending on the environment. These exposed areas with thin soils represent a harsh environment. Spurs and ridges have been linked to drier, shallower soils elsewhere (Vandvik et al. 2005). The exposure of ridge features (and slopes) was also linked to higher species richness in a study in Japan (Kubota et al. 2004). Spurs may be less exposed than ridges, depending on local conditions in relation to the direction of their descent from the ridge higher up. In colder environments, ridges also have relatively little snow and experience early melting, meaning a longer period without snow patches (Löffler 2005).
	Ridge (where two upward slopes converge)	
	Footslope (an upward slope extending from a flat area)	Footslopes provide heterogeneity alongside an otherwise relatively flat area. Their significance lies in both energy-related variables and moisture. In particular, they have been linked to prolonged snow cover and species' distributions in high latitude environments (Löffler 2005) and multiple countries in Africa, for example (Siebert et al. 2010; Rohde & Hoffman 2012). The ecological relevance of these features has also been highlighted in area where water is a key limiting factor via their effect on surface run-off (Kidron 2014).
	Shoulder (a downward slope extending from a flat area)	Somewhat comparable to footslopes, except shoulders will generally be more sheltered than footslopes. If descending from an open plateau, as shoulders often do, these features may provide a relatively sheltered, well-drained area that is more dynamic than that flat area above.
	Valley or valley-like feature (where two downward slopes converge)	Valleys come in many sizes, from gullies and dells (a small, wooded valley) created by small streams to vast u-shaped features created by glacial erosion. Coverage of valleys, in their broadest sense, was one of the more important geofeatures in a recent macroecological study of British vascular plants (Bailey et al. 2017). These features have also been reported to have significant effects of climate, through temperature inversions, for example, which has ecological implications because of effects on local weather, soil moisture conditions, and snow cover (Whiteman et al. 2004). Combined, valleys have great potential to affect species richness (Gould 2000; Ito et al. 2003). However, patterns within a valley can be complex,=: for example, species richness may be lower in a valley bottom compared to areas of higher elevation (Grytnes 2003). Overall, valleys provide much in the way of environmental heterogeneity.
	Saddle (a flat u-shaped depression between two peaks)	Saddles can create quite unusual conditions within the context of the broader landscape. These landforms typically have moister soils than the surrounding slopes, contain many pits (depressions). Depending on their aspect in relation to the prevailing wind, saddles can be more exposed and act as a funnel, or be more sheltered, and levels of solar radiation will also differ to the surrounding area (Litaor et al. 2008). Within a saddle, there may be many pit-like and hydrological features, increasing moisture and water levels, depending on drainage.

	Flat ground or plateau (questionable as to whether this is a 'feature', per se)	Flat ground is potentially overlooked in ecology, in favour of more topographically complex landscapes and features, if flat ground can indeed be considered a feature as it is here. Flat ground, however, may present a complex part of a landscape, often with increased human activity and, in less human-dominated areas, and it may be more susceptible to future environmental change because of limited .thermal variability compared to heterogeneous regions, depending on the place (Lenoir et al. 2013). Perhaps most importantly, flat features can represent places of high fluvial or glacial depositions (see 'surface materials' below), high runoff (Gallant & Dowling 2003), and active hydrological features. Meanwhile, flat areas at higher altitudes (i.e. plateaus) are often associated with unique environmental conditions and species (Klanderud 2010; Vetaas 1992; Odland 2010; Østbye et al. 2007). Few studies contrast plateaus with other features in terms of their species richness, but plateaus generally had higher biodiversity than the plains and slopes in such a study in southern Africa (Burke et al. 2003).
	Cliff or escarpment	Cliffs offer protection from predators and competitors for various plants, birds, and insects, for example, and might be especially relevant for protecting plants against grazing mammals (Hjort et al. 2015; Moore & Crawley 2014; Milchunas & Noy-Meir 2002). Areas with cliffs and escarpments may have very high species richness (Ingerpuu et al. 2003; Cole 1985; Thuiller et al. 2006; O'Brien 1993), sometimes because of the protection these features afford from human as well as natural activities, such as deforestation (Fox & Fox 2000) or management (Ingerpuu et al. 2003).
	Tor (free-standing relatively hard rock)	Rocky outcrops and tors' fine-scale environmental conditions can either offer preferable conditions to the surrounding area through shelter or can make for very harsh environments, both of which affect species' distributions and overall biodiversity differentially. On a mountain peak or plateau, tors can provide a refuge for organisms, amidst otherwise harsh environmental conditions (Wrightham & Kempe 2006). As with cliff faces, rocky outcrops may offer protection for plants against grazers (Milchunas & Noy-Meir 2002). This stability is important mobile species, as well: outcrops can provide stable habitat for vertebrates, such as mountain hares (Galende & Raffaele 2008). Outcrops can make for harsh environmental conditions and species that live in these places may need a stable seed bank and be adapted to soils that are thin, rocky, and low in nutrients (Seabloom et al. 2003). In tropical areas, compared to surrounding terrain, rocky outcrops at high altitude typically experience lower temperatures, low water and nutrient retention, high solar radiation, and strong winds (Medina et al. 2006) Outcrops have been reported as poorer in overall species richness but as hosting a greater number of endemic species in a study in Brazil (Medina & Fernandes 2007).
	Rocky outcrop (exposure of bedrock or old superficial deposit)	
	Sand dune	There is a wide variety of sand dunes across different environments. However, coastal sand dunes typically form bands associated with environmental gradients within which salinity and sediment mobility decrease away from the coast: this has significant effects for patterns of vegetation, with species more resilient to burial and sea spray nearer to the shore and shrubs and trees further inland (Hernández-Cordero et al. 2015). Burrowing animals may also thrive in dune environments and biogeomorphic feedbacks can be quite pronounced (Corenblit et al. 2011).

	Deflation surface	Deflation surfaces can be an unstable part of a landscape (Bamberg & Major 1968). These surfaces will often form on ridges (see above) and other exposed landforms and are inherently associated with harsh conditions within which only specialist species can survive.
	Terrace, kame terrace, and esker	As with many landforms, kame terraces and eskers provide local variation in aspect and elevation, but perhaps the most significant effect they have is on the soil and local hydrology. These features have been recorded as being well-drained, making for very dry soils (Silander & Klepeis 1999). The material components of terraces can have significant effects on surface and ground water movement and chemistry (Winter et al. 2008).
	Boulder-type feature (boulder field, erratic boulder)	The scale of applicability depends on coverage. For example, if there is a boulder field then similar ecological effects will be repeated across the landscape, but if it is an erratic, then unique landscape-scale environments may be produced. One of the most noteworthy effects of boulders may be as a refuge against grazers, as well as harsh environmental conditions (Moore & Crawley 2014).
Hydrological features	Lakes	The transitional environmental conditions at the interface between freshwater and terrestrial that lakes (of varying sizes) offer means that local biodiversity can be substantially benefitted, and lakes support a number of key ecosystem functions such as habitat provision and a source of food (Schmieder 2004).
	Rivers and streams	Much like lakes, key ecosystem functions include the provision of food and habitat. Rivers additionally, however, offer connectivity within a landscape for some species via riparian corridors, whilst representing barriers for others. The connectivity that rivers offer has been linked to alien species richness, for example (Deutschewitz et al. 2003; Bailey et al. 2017). Overall environmental heterogeneity created and maintained by river systems because of the high levels of geomorphological activity and effects on landforms (e.g. erosion) and land surface materials through flooding events, which provide suitable substrates for vegetation (Viles et al. 2008). These processes may be even more pronounced in high energy systems with steeper slopes (Hjort & Luoto 2010; Bendix & Hupp 2000).
	Ponds, springs and spring-fed headwaters	All of these features represent a key water resource to some extent and increase overall species richness via habitat provision for freshwater species (e.g. amphibians) and via effects on local-scale soil, moisture, and nutrients. Hot springs have been noted as especially important and have a 'disproportionate ecological role' by providing unique chemical and surface material conditions (e.g. nutrients, texture) because of their effect on local edaphic and microclimatic conditions (Hjort et al. 2015; Smith et al. 2003). Cold springs have also been noted for the ecological importance associated with their hydrological stability and temperature regulation in otherwise unstable environments (Scarsbrook et al. 2007). However, ephemeral ponds and springs can produce a nutrient regime that benefits some plant species (Hjort et al. 2015). These may form in pit-like features.
Land surface materials	Parent material	Not necessarily a surface material unless exposed, but with climate, topography, hydrology, and organic activity, bedrock produces the parent material for soil, which can ultimately affect the physical and chemical properties (below). Geological age has also been linked to weathering, erosion, and disturbance processes, as well as overall heterogeneity (Otto et al. 2016). Studies into the effect of parent material on ecological patterns are particularly extensive in the tropics (Bern et al. 2005; Yavitt 2000). Indeed, classifications of

		parent material may be more ecologically relevant than soil maps (Theobald et al. 2015) because of the many associated general properties, such as limiting nutrients (Augusto et al. 2017; Niskanen et al. 2016). Also note that parent materials can be superficial deposits (see below).
	Soil or surface texture	Strongly influenced by parent material (see above). Physical soil properties have implications for run-off rates, which can affect the stability of an environment or landscape (Kidron 2014). These effects may be especially pronounced around glacial and fluvial deposits (Winter et al. 2008). Many soils provide a substrate that burrowing animals can use for shelter (Viles et al. 2008). Meanwhile, depending on the environment, it has also been reported that albedo may be substantially affected by surface material in some environments (Scull et al. 2005). In turn, this can affect near-ground air turbulence, net radiation, the warming of the soil and air for evaporation, and therefore humidity. As well as affecting photosynthesis, these factors can affect local thermal convection, which is of particular relevance to insects (Stoutjesdijk & Barkman 2014).
	Soil chemistry (pH and mineralogy)	Strongly influenced by parent material (see above). pH and chemistry can act as key limiting factors in ecological communities (Ste-Marie & Paré 1999; Harter 1983; Gould & Walker 1999; Lechowicz & Bell 2016), whilst increases in pH and nitrogen have both been recorded in relation to disturbance events in caused by hydrological features (Vandvik et al. 2005).
	Tufa	Calcium carbonate deposits can provide habitat for various microbes, bryophytes, and diatoms (Hjort et al. 2015; Stougaard et al. 2002).
	Peat: bogs and fens	These represent features with different hydrological regimes. A water surplus typically exists in these areas, which can affect the moisture gradient of the nearby area as well (Löffler 2005). Boggy environments support many specialist species, but may too harsh for others, meaning that effects on overall biodiversity can be complicated. Bogs are typically slightly elevated, have a low pH, low levels of inorganic solutes, and low species richness, whilst fens, which are concave in topography, support higher species richness because of the higher pH and higher nutrient concentrations (but these may still be below those of the surrounding area), according to a study conducted in Canada (Reeve et al. 2000). Conditions will vary dramatically from place to place.
	Superficial deposits	The geographic spread of superficial deposits is generally patchy within relevant landscapes but, where they occur, they can have substantial effects on hydrology, and soil texture and chemistry. For example, in Derbyshire, England, superficial glacial deposits of loam, gravel, and clay themselves provide a parent material for soil (Pigott 1962). Superficial deposits can produce 'outliers' of land surface material within a landscape (Rayner 1913), affecting species' distributions and overall biodiversity. As well as cases of supporting a given species' distribution, superficial deposits comprising wind-blown sand have been linked to areas with a very limited number of plants because of harsh conditions (Farrow 1917)
	Glacigenic till and moraines	Glacial deposits have not only substantial effects on local hydrology (Winter et al. 2008) and vegetation distributions, such as moraines In Swedish Lapland (Darmody et al. 2004) and specific shrubs to lateral moraines in the Alps (Eichel et al. 2016). Till and moraines

	can produce ridge-like landform features, with properties in line with those described above for ridges.
Permafrost	Permafrost areas relate to specific plant communities but the dynamics are complicated and not fully understood (Bakalin & Vetrova 2008). Links between vegetation and permafrost are being realised more fully than even before with global warming and the associated degradation of the permafrost. For example, in Alaska, birch forests seems to be decreasing as fens increase with thermokarst development and associated changes in microtopography (e.g. formation of pits and gullies) and redistribution of water resources leading to wetting in the depressions and drying on the higher ground (Jorgenson et al. 2001; Osterkamp et al. 2009). Inclusion of permafrost as a geofeature in ecological analysis should be done with care, considering these rapid changes.

Geodiversity and the ecological niche

Hutchinson's (1957) concept of the ecological niche links the geographic distribution of species (mobile and sessile) to the environment (Thuiller et al. 2013). Whilst a complex term, the 'niche' essentially aims to describe the combination of factors that enable a species to exist in a given place (geographic region and biotic community) and how a species affects the abiotic environment (Peterson et al. 2011). Here, heterogeneity is important via the provision of more niches or because of partitioning across the spectrum of heterogeneity (Wilson 2000). The so called 'BAM framework' (biotic [B], abiotic [A], and organism movement [M]) recognises that an organism's occupied distribution (i.e. the realised niche) is determined by the overlap of suitable biotic and abiotic factors within the range of an organism's dispersal area (Peterson et al. 2011). A further potential distribution (the invasible distributional area) is within the required biotic and abiotic environmental conditions but has not yet been colonised (i.e. the potential niche).

Ambient conditions and usable resources constitute the abiotic (A) environment from an ecological point of view (Lavers & Field 2006). Both may be competed for, but *ambient conditions* (e.g. light, pH, water) are not depleted in the way that *usable resources* (e.g. minerals) are. The balance of this may vary depending on the particular local conditions. Geodiversity includes elements of both *ambient conditions* and *usable resources* because, for example, land surface materials relate to finite *usable resources* (e.g. nutrients) that organisms compete for. Meanwhile, microclimatic ambient microclimatic *conditions* resulting from landforms, for example, are not depleted by organisms, but may still be competed for, depending on usable resource availability. This trade-off of usable resources and ambient conditions should theoretically be influenced by the local geophysical environment once coarse climatic and topographic filters have been passed.

Within the BAM framework, geodiversity also has the potential to affect biotic (B) conditions and organisms' movements (M). A cliff face, potentially diverse in nutrients, geology, and soil, provides a prime example. Cliff specialists face reduced competition from generalist species because some cannot disperse to or establish and persist in such a place. Examples of sessile and mobile taxa that are cliff specialists include: *Bembidion saxatile* (a beetle) (Telfer 2006); *Fratercula arctica* (Atlantic puffin); *Draba aizoides* (a wildflower). Dispersal may be aided by rivers, particularly for alien plants (Deutschewitz et al. 2003), but rivers may also provide a barrier to some mammals. Landscape configuration can also affect species' movement and dispersal, along slopes for example (Rhodes et al. 2014).

The variability of niches through time but within a given space must also be considered. One of the key drivers of this short-term resource variability is seasonality, especially in low energy environments (Parks & Mulligan 2010). Seasonality could provide a climatic filter determined by the lowest level of energy-related resources on an annual cycle (e.g. mean temperature of the coldest month; minimum rainfall of driest month). Differential spatial and temporal resource provision once this filter has been passed, however, is largely mediated via environmental heterogeneity (Stein et al. 2014). The value of relatively crude environmental heterogeneity variables is not being brought into question by geodiversity research because we know such variables to be important. Indeed, standard deviation in elevation and other such variables have been related to increased niche space and temporal stability (Thuiller et al. 2006; Bailey et al. 2017; Field et al. 2009). Relatively crude topographic variables (e.g. aspect, slope, and elevation), however, will generally be related more strongly to climate (Bailey et al. 2017). These topographic variables may therefore have less relevance in the context of temporal niche variability than geofeatures, which operate beyond climate- and energy-related parameters, and may buffer against some of these broader-scale changes (McLaughlin et al. 2017; Keppel et al. 2015). Though, more generalised topographic data (TWI and slope angle) have been also been successfully linked to refugia in Finland, for example (Niskanen et al. 2016).

Geofeatures may therefore relate to temporal dynamism of niches within a landscape and affect patterns of life (biodiversity and species' distributions). One example would be the presence of an ephemeral stream or pool that is periodically flooded: some plants require such conditions to thrive (Hjort et al. 2015). More commonly, dynamism may be produced by slope-related geomorphological disturbance processes, which we discuss further below. On the other hand, geofeatures are able to provide relatively stable conditions through time. For example, consider a hollow or gully in a mountainside. These may buffer against warming temperatures to ensure that cooler and moister conditions, and even snow patches, can persist through

spring and summer (Harshberger 1929). Conditions in and around these geofeatures may be harsh at times (but still stable), excluding most species: marshes, hot springs or spring-fed headwaters (Hjort et al. 2015) are capable of providing stable niche space through time in a given place, even when it is a relatively harsh environment that may exclude generalists from establishing there (Lavers & Field 2006).

Ecological strategies

We do not wish, and nor is it necessarily advantageous, to tie geodiversity to any single existing ecological framework or theory beyond that of the ecological niche. CSR has its associated contentions, which are summarised elsewhere (Wilson & Lee 2000). However, we see value in discussing these theorised links, which can be then criticised in future geodiversity research, and much of this part of our discussion is also applicable to species' traits more generally. CSR defines plant species in relation to the extent to which they belong to each of three primary functional strategies (secondary strategies are not explicitly considered here): Competitor (C), Stress tolerator (S), or Ruderal (R), which are species that persist in areas of high interspecific competition, resource-poor environments, and environments with a high level of disturbance, respectively (Grime 1974; Grime et al. 2014; Grime 1977). As with much of the ecological theory discussed so far, spatial scale is key: these factors will largely be relevant only after climate and climate-related geofeature (e.g. elevation) filters have been considered. To our knowledge, so far CSR–geodiversity links have been considered only briefly, in relation to landslides and soil mineral availability (Matthews 2014).

Land surface materials (often in combination with hydrological and geomorphological features) are likely to be of the greatest importance for competitors, via the provision of minerals, nutrients and the ambient pH (Hjort et al. 2012), as well as moisture levels and drainage due to soil type and texture (Cosby et al. 1984; Vereecken et al. 1989; Nichols et al. 1998). If the quantity and quality of these factors are sufficient, environmental stress will be limited and competitive species should thrive, given other environmental conditions are met (e.g. climatic). On the other hand, limits to moisture, very high or low pH, or lack of a given mineral, for example, will result in conditions that are stressful to many species, probably resulting in low productivity environments (Grime 1977). Here, competitors may give way to stress-tolerant species that are much better at coping with these conditions. Extremes of stress-tolerant species include metallophytes (Serrano et al. 2013) and halophytes (Flowers & Muscolo 2015), for example, which can tolerate stressful environmental conditions imposed by land surface material properties. Additionally, CSR has been explicitly linked to substrate and succession processes in glacial environments (Caccianiga et al. 2006). Here, till deposits

high in nitrogen supported faster growing species that were able to overcome disturbance (R), whilst stress-tolerant (S) species that could use nutrients more efficiently were more successful in late-succession areas that were low in nitrogen (also see Gentili et al. 2010).

Landforms may have importance in the context of CSR beyond their effect on land surface materials. As discussed in relation to the ecological niche above (and see Table 3), landforms can have stabilising effects on the environment, which may limit extreme conditions and support the presence of competitive species (Virtanen et al. 2010; Caccianiga et al. 2006). Alternatively, certain landforms create more stressful, exposed, or unstable conditions (e.g. deflation surfaces; ridges) in favour of stress-tolerant species, or dynamic environments (e.g. rivers; slopes), which could disadvantage competitor species in favour of ruderals (Gentili et al. 2010). This may be especially pronounced for pioneer species in glacial environments, for example (Corenblit et al. 2015).

Theory surrounding the r-K continuum is also likely to be of relevance here, and indeed parallels were drawn when CSR was developed: the r- and K-selection extremes were considered to be related to ruderal (R) and stress-tolerant (S) strategies, respectively, with competitor (C) species in between, within the primary strategies framework (Grime 1977). However, explicit links have not been drawn between r-K theory and geodiversity or geofeatures, so far as we are aware, despite theoretical relevance, particularly in terms of an environment's stability (Glazier & Eckert 2002). Pioneer species in the example above will typically favour high reproduction rates and short lifespans (r-selection), whilst species in more stable environments (e.g. landforms that provide shelter such as hollows) are likely to have longer lifespans and produce fewer offspring (Pianka 1970). Species with longer lifespans occupying stable environments may also be better competitors (Glazier & Eckert 2002). Geophysical conditions therefore have the potential to elicit significant effects on plant communities by affecting the traits and strategies of the species that can survive around or on a given landform or surface material.

Table 3 Linking primary CSR strategies to geodiversity and geofeatures. Within the CSR column, the typical environmental conditions that a plant in this category would prosper in are given. This table does not account for the continuous scores that are usually used for CSR classifications whereby species may below to multiple categories.

Primary CSR category	Typical species' traits	Relevance to geofeatures (examples)
Competition (low stress; low disturbance)	Phenotypic plasticity; rapid growth rate; lateral spread	Surface materials: provision of high levels of minerals and nutrients; effects of soil type and texture on moisture and hydrology Landforms: Sheltering effects create more stable conditions (microclimatic; hydrological); effects on localised light availability.
Stress (high stress; low disturbance)	Efficient nutrient retention; slow growth rate;	Surface materials: parent material that results in unique mineral combinations or lack of minerals Landforms: presence of exposed landforms attracting specialist species (e.g. cliff faces; snow patches in hollows; exposed ridges)
Ruderals (high disturbance; low-stress)	Short life cycle; high seed production	Landforms + Materials: Hill-slope processes in combination with hydrological features and soil properties can create disturbance events, creating niche space; ephemeral hydrological features and processes create disturbance (pools, streams).

Disturbance processes

Disturbance processes are likely to be relevant for finer-scale species' distributions, species richness, abundance, species interactions, and ecosystem productivity, and functioning, largely via the impact on habitat heterogeneity and resource availability through (Le Roux et al. 2013) and via the creation of novel environmental spaces that can be readily colonised (Hjort et al. 2012; Benton 2009). More intense disturbance events will produce greater selection pressures on the ecological community (Grime 1977). Measured geofeatures may be able to allow us to implicitly incorporate these processes in some environments (Hjort et al. 2012). For example, snow and geomorphic (relating to soil, movement speed, deposit age, and vegetation cover) disturbance indices have been used to significantly improve models of species' distributions for some plant species in a relatively fine-scale alpine study (Randin et al. 2009). The snow and geomorphic disturbance variables improved models for 23 and 19 species, respectively (out of 92 species). However, whilst model fit was improved, predictive power was not, probably because of the coarseness of the disturbance variable used (Le Roux et al. 2013; Randin et al. 2009).

Building on Randin *et al*.'s work, Le Roux *et al*. (2013) identified the potential importance of geomorphological disturbance for fine-scale vascular plant, lichen, and bryophyte distributions in Finland and Norway. Here, two geomorphological disturbance

variables (terrestrial and fluvial) improved models for most (124 of 154) species distribution models across vascular plants, bryophytes, and lichens. Meanwhile, a positive relationship between species abundance and composition, productivity (using the normalised difference vegetation index; NDVI), and geomorphological disturbance has been noted over a period of 26 years in north-west Finland (Virtanen et al. 2010). Here, it was reported that disturbances may have changed the competitive environment and rendered the community less stable and more susceptible to colonisation. However, disturbance processes beyond geomorphological, such as anthropogenic and biotic (e.g. burrowing, grazing) are also important, and it has been suggested that landforms can affect non-geomorphic disturbance agents such as fire and grazing (Swanson et al. 1988). The applicability of disturbance events geographically and taxonomically requires further research because most work thus far has been conducted in high latitude and/or high altitude environments. We also need to recognise the complex nature of disturbance events, which are seldom linear (Viles et al. 2008), and the extent to which geofeatures have the potential to allow us to implicitly incorporate these disturbance events in our models in different environments.

Sheltering from grazers

Certain geofeatures can explicitly identify locations that provide shelter to sessile species from either harsh abiotic conditions (e.g. rocky outcrops provide relatively moist and calm conditions compares their vicinity; multiple examples are detailed in Table 2) or grazing animals, in a way that metrics relating to elevation and slope cannot. The effect of grazers on plant communities remains an open question, with different responses between plant groups, environments, and grazers. This natural exclusion of grazers by geofeatures has been quantitatively demonstrated. For example, a recent study in northwest Scotland showed that on boulders inaccessible to red deer, heath communities benefited, which had cascading effects on bryophytes and lichens: bryophyte cover increased and saxicolous lichen cover decreased. (Moore & Crawley 2014). However, lichen species richness has generally been found to be lower in sheep-grazed areas in upland Britain (Fryday 2001).

The overarching protective, refuge effect that geofeatures provide for plants has been noted in a meta-analysis as a specific evolutionary strategy of avoidance in a (Milchunas & Noy-Meir 2002). In Milchunas & Noy-Meir, 'physical impedances' (refuges) includes cliff faces, rocky outcrops, gulley, and boulder tops at the finer scales (86% such features reported positive effects in relation to plant diversity), whilst mesas and islands may be considered at broader scales (50% had a positive link to plant diversity). Furthermore, the combined effects of protection and microclimate and fine-scale abiotic factors heavily promote abundance in some

species. However, grazing can act as a beneficial disturbance process and create ecological opportunities (Vandvik et al. 2005) and lower plant diversity has been recorded in the absence of grazing in St Kilda (northern Outer Hebrides, Scotland) because of the grazers' effect on the dominant grass species (Crawley et al. 2004), for example. Therefore, geofeature protection may not always benefit overall biodiversity.

Refugia

One key application of this capacious literature on geofeature–species relationships might lie in refugia, which define suitable spaces in the landscape within which species can retreat to during periods of unsuitable broad-scale environmental conditions (e.g. climate), before redispersing once suitable conditions resume (Keppel et al. 2015; Niskanen et al. 2016). These spaces in a landscape provided by geofeatures have been linked to sites of long-term refugia, as well as the more short-term refuges from grazers, as we discussed above. Mountains in particular are known to host a great many refugia because of their geodiversity and the associated suitable pockets of environmental and geographic space offered by geofeatures (Gill et al. 2015). Steep landforms have been identified as especially important spaces for refugia in northern Europe (northern boreal to the Arctic-alpine zone) and their 'vital' role for allowing species to persist into the future highlighted, as the climate changes (Niskanen et al. 2016). The authors here also noted the potential significance of these steep landforms in relation to disturbance processes, and for these to affect refugia. Geology data were less important in Niskanen et al.'s study. However, soil chemical and physical structure may be significant for refugia through effects on the temporal variability in soil and air temperature, water holding capacity, and moisture availability (Lenoir et al. 2016). Indeed, the value of hydrological features in the provision of refugia and microrefugia must not be overlooked: microenvironments with high relative water availability are generated by hydrological processes and these have been linked to species-specific refugia (McLaughlin et al. 2017).

Geofeatures' ecological relevance

Land surface materials

Clearly, there are interrelations between different aspects of geodiversity and intimate connections exist between hydrological features and landforms, most of which are physically underlain by, and interact with, the land surface materials (geology; parent material; glacial and fluvial deposits; soil). These will vary tremendously according to the study area. Land surface materials, however, are amongst the best-studied aspects of geodiversity. Existing research is spread across many different ecosystem types and climates and has a relatively

long history (e.g. Bamberg & Major 1968 note the importance of calcareous parent material for vegetation communities). In general, surface materials are ecologically relevant because of their chemistry and physical structure, which affects pH, mineral presence, moisture levels, substrate texture, and the richness of these things in a given area. In turn, these properties relate to resource availability and habitat variety (Hjort et al. 2012). The parent material (and secondarily soil weathering and landforms) is key in limiting levels of phosphorus (Augusto et al. 2017; Vitousek et al. 2010; Mage & Porder 2013) and has greater ecological relevance than some soil classifications (Theobald et al. 2015). Data on geological age may also be very useful because of interactions with topography and dynamic processes such as erosion (Otto et al. 2016). Specific land surface material categories, and their theorised ecological relevance, were detailed in Table 2.

Soil type, moisture, and temperature are, to varying extents, the product of climate, topography, hydrological processes, and land surface material properties (Kuglerová et al. 2016; Hagemann & Stacke 2014). Some of these ideas were introduced some time ago (see Jenny 1941 on CLORPT). Gradients in soil moisture have been closely linked to hydrological niches and structuring of vegetation communities in alpine grasslands (Garcia-Baquero et al. 2016), for example. Indeed, interactions between hydrology and land surface materials are extensively reported in boreal and temperate systems, fluvial disturbances and processes have been linked to changes in soil chemistry and specifically increase in pH and nitrogen content with increased disturbance (Kuglerová et al. 2016). Meanwhile, deeper soils with poor drainage (and therefore higher moisture) have been associated with the presence of heath communities in Norway, for example (Vandvik et al. 2005).

Because of the fundamental nature of nutrients to plant growth, which then has impacts throughout the ecosystem, identifying the source of nutrients is essential (Niskanen et al. 2016) and parent material geofeatures may allow for the identification of nutrient sources. For example, a study in a Costa Rican tropical forest identified parent material weathering as the dominant nutrient source (Bern et al. 2005), whilst the presence of alkaline parent materials at a site in Sweden has been identified as giving rise to a higher content of calcium and magnesium, which are important for soil fertility (Vestin et al. 2006). The value of explicitly recognising parent material type has also been noted for high latitude sites (Walker 2000) and elsewhere. The underlying rock and the soil it produces can affect relatively fine-scale individual species' distributions (demonstrated in PAPER IV). For example, ultramafic soils derived from igneous rocks have been linked to a species of plant in South Africa (Siebert et al. 2010). More generally, soil nutrients have been linked to patterns of tropical tree distributions (John et al. 2007), tropical forest diversity (Townsend et al. 2008), Mediterranean woodlands,

possibly via phosphorous limitation in granitic soils (Kooijman et al. 2005), forests on a limestone rock exposure (Ingerpuu et al. 2003), landscape-scale vegetation distribution is Swedish Lapland (Darmody et al. 2004), and dryland microbial communities (Steven et al. 2013), to list just a subset of such works.

On balance, land surface materials have at least some effect on much of life on earth and their ecological links are widely reported (further examples, including for glacial deposits, are included in Table 2). However, land surface material diversity metrics, which included superficial deposits, bedrock types, and soil texture, are not necessarily amongst the most important geodiversity components when placed alongside topography and climate at landscape, regional, and national scales (Bailey et al. 2017).

Landforms

Landforms can affect the abiotic environment and resource gradients via microclimatic conditions, fine-scale air movements, hydrology, moisture levels, pH, solar radiation, and mineral and nutrient availability and diversity (Swanson et al. 1988; Lawler et al. 2015; Löffler 2005). Landform effects on moisture may be especially relevant in some environments. For example, higher moisture levels can be found in pits in the landscape, given suitable soil and limited drainage, whilst exposed areas (e.g. ridges) are often lower in moisture (Kubota et al. 2004). This moist environment may provide a suitable habitat for some species in an otherwise dry landscape (Milchunas & Noy-Meir 2002). Landforms can also protect organisms against grazing mammals affect the movement of grazers in a landscape (Vandvik et al. 2005), as well as promote disturbance processes (Le Roux et al. 2013), both of which we detail below. Exposure is a key factor of ecological interest regarding landforms: contrasting vegetation communities may be seen on the stoss (windward) versus lee side of a landform (Jonasson et al. 2005). Few studies compare multiple landform types, but one study suggests that observed differences in species richness between valleys, slopes, and ridges was due to habitat preferences and shade/drought tolerance (Kubota et al. 2004). Meanwhile, broad-scale patterns of native and alien species richness have been explicitly linked to valleys, hollows, and other landforms (Bailey et al. 2017).

Hydrological Features

The heterogeneity that fluvial systems provide makes them one of the most productive in the world (Corenblit et al. 2015). Here, we focus on explicit hydrological geofeatures (see Table 2 for a full list of hydrological features), which affect the flow of water through a landscape, and water bodies (e.g. lakes, ponds) and sources (e.g. springs), rather than the effect of hydrology

on soil moisture, which we have discussed above. We recognise the explicit links between hydrology and land surface materials, however, whereby soil moisture is the product of climate, topography, hydrological processes, and land surface material properties (Kuglerová et al. 2016; Hagemann & Stacke 2014). Indeed, in addition to rivers affecting species' occurrences via moisture, species' occurrences and higher species richness have been directly linked to rivers through flooding (Van Looy et al. 2003) and the associated creation and destruction of substrate, and landscape connectivity and the transport of propagules (Bendix & Hupp 2000). Additionally, broad-scale patterns of alien plant species have been linked to rivers (Deutschewitz et al. 2003; Bailey et al. 2017). At the landscape scale, fluvial feature richness (channels, lakes, gullies, cutbanks, and deltas) has itself been connected to increased overall geodiversity (Hjort & Luoto 2012).

Meanwhile, springs and spring-fed headwaters help to maintain temperature and water-flow and provide a range of chemical conditions: springs may be especially important in desert environments (Hjort et al. 2015) but cold springs in temperate climates have also been noted for their biodiversity (Scarsbrook et al. 2007; Smith et al. 2003). All hydrological features therefore maintain environments on their banks and shores that are not generally available in the wider landscape, thus supporting higher levels of biodiversity (Schmieder 2004; Crawford & Semlitsch 2007). As well as affecting species richness, species' abundances may also be higher around these geofeatures because of access to both terrestrial and freshwater resources (Hjort et al. 2015).

Prospect: Integrating Geodiversity and Ecology

There is much existing ecological theory that is directly applicable in the context of geodiversity and geofeatures and we have, for the first time, compiled and assessed much of this information in one place with the purpose of advancing our conceptual understanding of geodiversity in ecology. The existing theory supports our geofeature definition ("a spatially explicit landform, hydrological feature, or land surface material that is homogeneous within a limited spatial scale, whilst providing heterogeneity across a larger area, and potentially through time") and geodiversity definition ("the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms"), which recognise the importance of explicitly quantifying these aspects of the geophysical landscape to better our ecological understanding (also see Bailey et al. 2017). Herein, we consider some existing shortfalls in geodiversity research to date, and respond to these towards informing future directions. These areas include: scale (spatial and temporal), to which our response is a spatio-temporal framework; the need for a consideration of biogeomorphology; climatic change;

availability of data and techniques; and caveats regarding the use of geodiversity in conservation and ecology more generally.

Towards a spatio-temporal, cross-scale, cross-taxa framework for geodiversity

Vastly different results may be obtained according to the spatial scale at which an ecological study is conducted (Willis & Whittaker 2002; McGill 2010; Hawkins et al. 2003; Whittaker et al. 2001). This matter has been only partly explored within geodiversity research (Bailey et al. 2017). Meanwhile, geodiversity work thus far has typically been conducted: (i) in temperate and high altitude and latitude environments; (ii) using static, present-day patterns of species richness; (iii) and mostly for plants. In short: we currently have an underdeveloped appreciation of the spatial, temporal, and taxonomic limits of the geodiversity concept in ecology and conservation, and fundamental scale theory from the biogeography literature is lacking.

At local scales, species richness and within-habitat conditions are affected by fine-scale abiotic and biotic interactions occurring on scales less than 100 years, whilst at continental and global scales, glacial-interglacial cycles, mountain building events, and sea level change (for example) occurring over millions of years lead to broad-scale biogeographic patterns (Willis & Whittaker 2002; Hawkins et al. 2003). Furthermore, at the landscape scale, species richness is thought to be principally affected by soil and topography over periods of 100 to 1,000 years. Energy and water availability and area, which have shaped patterns over the past 10,000 years, are most relevant at the regional scale for species richness. For individual species' distributions, climate is central at local (microclimate) and global scales; species interactions at local to sub-continental scales; habitat at landscape and regional or biome scales; and dispersal at least at local scales and beyond the biome scale (McGill 2010).

Spatial scale

Theoretically, at what spatial scales are geofeatures and geodiversity most applicable to ecological patterns, where 'scale' refers to both grain size (resolution) and extent (spatial scope of a study) (Hawkins et al. 2003)? It entirely depends on the geofeature being considered, and there will be variation for any given geofeature (e.g. valleys vary tremendously in size). However, broadly speaking, and given the existing frameworks discussed above, most geofeatures should be relevant at the local to regional extent and for smaller grain sizes, especially at the landscape scale (Bailey et al. 2017). Heterogeneity is generally thought to operate most strongly at these scales (Stein et al. 2014) and geodiversity is one aspect of heterogeneity. The balance between geofeatures and geodiversity will probably be strongly

affected by grain size. Consider a large grid cell (i.e. a coarse grain size): this is likely to contain greater environmental heterogeneity (e.g. range in slope and elevation) and greater geodiversity (more geofeatures) than a smaller grid cell. However, for explicit geofeatures mapped individually and their areal size (for example) incorporated into a dataset, their effect might be more pronounced in studies using a smaller grain size because of increased between-cell variation, especially if species' distributions are being modelled rather than species richness (Bailey et al. 2017).

Temporal scale and the effects of climate

The temporal dimension requires special attention in the context of geofeatures and geodiversity: geomorphological, hydrological, and geological features in the landscape are plastic, to varying extents, and their spatial coverage and ecological relevance changes through time, as too does their diversity. Climate in particular has the potential to alter geofeatures through time, and their associated processes, both directly and indirectly (Viles et al. 2008; Brazier et al. 2012). In the short- to medium-term, these changes can occur on interannual, decadal, and multidecadal timescales (Viles & Goudie 2003), whilst longer-term climatic and geological events are also important (Gill et al. 2015; Kubota et al. 2015). Longer-term processes typically relate to sea-level change, glaciations, ocean current changes, and mountain building events, for example, whilst short- and medium-term processes might affect slope instability and disturbance or mass movement events, hydrological processes such as flooding and gullying, and dune formation. The short- and medium-term impacts will vary from place to place, between geofeatures and spatial scales (Brunsden 2001), and are complicated by human activity and tectonic influences (Viles & Goudie 2003).

Climate-driven changes can affect species' distributions and biodiversity because of the links between geofeatures and organisms as an addition to any direct climatic effects on ecological patterns because of temperature change and thermal tolerances. Soil provides a clear example of these direct and indirect effects: climate change might impact a soil indirectly by affecting soil functions and processes (including those relating to erosion and disturbance) or directly through temperature and precipitation changes affecting chemical reactions, microbial communities, and moisture content (Brazier et al. 2012). Meanwhile, if a soil were to become drier, this could affect desiccation and increase the chance of soil erosion from wind, creating exposed surfaces. These direct and indirect effects from climatic changes have the potential to affect many of the theorised ecology-relevant processes listed in Table 2, through impacts microclimate, sheltering, and physical and chemical soil properties.

Climatic (and other) impacts may also affect a present-day landscape after they occur because of lag and legacy effects. This has recently been discussed in the context of drylands, where substantial ecological–soil–geomorphic legacy effects operating from days to millennia were reported (Monger et al. 2015). For example, as the authors discuss, in the medium term (years to decades), drought episodes, improper irrigation (human influence), and the presence of bare ground affected net primary production (ecological effect), salinity (soil), and gully networks (geomorphic), respectively. Other examples provided include the effects of rainfall on soil moisture recharge in the short term (days to months) and climate change on soil $CaCO_3$ dissolution in the long term (centuries to millennial). The magnitude of the original event, the time since its occurrence, and the sensitivity of the system all related to the reported legacy effects therein. Mountain systems, meanwhile, contain legacy effects of past glaciations, which had a substantial effect on present-day landform assemblages, for example (Jonasson et al. 2005).

These works highlight clearly why the temporal dimension is so important in some systems and places. It is also pertinent to consider, however, that geomorphological and geological processes also vary through time more separately from climate because of internal processes (Brunsden 2001; Viles & Goudie 2003; Miller et al. 2003; Eichel et al. 2016) and the idiosyncrasies of one's study site should be considered in this context. With more frequent and stronger extreme climatic events such as droughts and floods expected in the future (e.g. Le Roux et al. 2013), taking these processes into account as part of the dynamic landscape is going to become increasingly important.

Proposed spatio-temporal framework

Towards the development of an enhanced understanding of scale and geodiversity, we have combined two existing frameworks for species richness (Willis & Whittaker 2002) and species' distributions (McGill 2010). We demonstrate how researchers may wish to present their focal geofeatures therein (Table 4), which is discussed as part of a broader workflow below. Our aim is to provide a basis upon which to build quantitative studies, which will be needed to reveal these patterns more fully. A previous study has attempted to link scale to geodiversity (Lawler et al. 2015), but this effort lacked incorporation of explicit geofeatures and time, making it difficult to use effectively. Therefore, we consider our efforts to be a worthwhile advancement that will benefit ecologists and geodiversity research. Our framework (below) does not explicitly link to place (i.e. where is geodiversity most important, geographically?) and taxa, but these should remain key considerations going forwards.

Table 4 Our cross-scale geodiversity framework, building on Whittaker and Willis' (2002) by incorporating example geofeatures and associated processes and temporal variability. There is a distribution of sizes for all features (e.g. a small valley would be relevant at the local scale, whilst a large u-shaped valley could be ecologically relevant up to the regional scale). Therefore, the examples given are generalised: quantitative studies would use specific examples with measured features. [1] Elements of McGill (2010); [2] Estimations informed by other sources (Eichel et al. 2016; Gill et al. 2015) and referring to general feature stability: e.g. for a cliff, rock falls occur annually, but at the landscape scale this unlike to affect ecological patterns, whilst erosion and weathering over thousands of years are likely to have a greater effect.

Approximate spatial extent (km^2) Scale of species richness	**Example geofeature**	**Example of key species distribution controls at the relevant scale, which will vary between places [1] (also see Table 2)**	**Temporal scale of feature's stability (years) [2]**
Local and plot scales (<10^2) **Within-community and within-habitat.**	Boulder	Shelter provides a refuge from harsh climatic conditions (stable microclimate) and grazers (prevents biotic interaction).	< 100
	Moraine	Associated soil textures and raised elevation affect hydrology, creating drier substrate.	< 100
	Coastal sand dune	High salinity and exposure if on the shore-side of a dune system	< 100
	Spring	Provision of stable habitat and microclimate.	< 1,000
	Cliff	Protection from predators; isolation from competitor species.	< 5,000
	Peat bog	A water surplus and low pH create a specialist environment.	< 5,000
Landscape (10^2 – 10^4) **Species turnover within a landscape and between-community richness.**	Slope	Increase solar decreased solar radiation affects energy input; disturbance events (e.g. landslide) promote presence ruderals.	< 1,000
	Ridge	Exposure produces locally dry, thin soils only suitable for specialists.	< 1,000
	Hollow	Shelter and hydrology provide unique niche space and habitat within a landscape.	< 1,000
	Stream	Connectivity within a landscape promotes species' dispersal; disturbance promote community composition changes.	< 1,000
	Saddle	Shelter from prevailing wind conditions and provision of a large depression within the broader landscape, which has moist soils.	< 5,000
Regional and above (10^4 – 10^5) **Species richness of large areas, with evolutionary effects for the largest**	River system	Connectivity across large areas allows for dispersal; riverine habitat provision.	< 10,000
	Parent material	Broad-scale effects on nutrients and pH.	> 10,000
	Plateau	Large plateaus can have regional relevance if they operate as islands	10,000 +

Geodiversity across taxa and places

Where do the geographic limits extend to (in terms of place) for the geodiversity concept? And is geodiversity equally applicable to terrestrial sessile and mobile taxa? The limited body of work on geodiversity makes it difficult to generalise and further work is needed, which is why we have not explicitly incorporated location and taxa into our framework. However, the research thus far is suggestive. There is evidence for the role of geofeatures and geodiversity in temperate (Bailey et al. 2017; e.g. Anderson & Ferree 2010; Bétard 2013), high latitude (Tukiainen, Bailey, et al. 2017; Tukiainen, Alahuhta, et al. 2017; Hjort et al. 2012; Virtanen et al. 2010), and high altitude (Jonasson et al. 2005; Dufour et al. 2006) environments, and, more rarely, in sub-tropical (e.g. Kubota et al. 2004) and tropical locations (e.g. Barthlott et al. 2007). The role of human activity is also likely to be important, and this itself may affect geodiversity and biodiversity (Tukiainen, Alahuhta, et al. 2017).

Such studies incorporating geodiversity have mostly been conducted for plants, revealing a general relationship with geodiversity (Hjort et al. 2012; Anderson et al. 2015). In particular, geodiversity may be more important for native than alien vascular plant species richness across multiple scales (Bailey et al. 2017), whilst in Finland, geodiversity was more important for threatened vascular plants and bryophyte species richness than molluscs, lichens, and mammals at a macroecological scale (Tukiainen, Bailey, et al. 2017). Theoretically, sessile species may be more relevant within the context of geodiversity than mobile species because of their intimate connection with land surface materials, hydrological features, and landforms (Gray 2013). The relevance for mobile species, beyond their biotic interactions with sessile species (e.g. insects tracking plants up an elevation gradient with climate change), may be more nuanced and rely on different types of species-landscape interactions (e.g. behavioural) than those discussed for sessile species (need for nutrients and buffering from environmental conditions, for example).

Shelter is a key environmental condition provided by geofeatures: we discussed in our assessment how cliffs provide habitat and protection for bird species. Therefore, biodiversity models for certain bird families might be improved by an understanding of cliff-type geofeatures. Meanwhile, fine-scale geofeatures are likely to be utilised by a number of species because of microclimatic effects. Butterflies, for example, might respond to climatic changes behaviourally by seeking new spaces, as defined by landforms, within a changing landscape (Dennis & Sparks 2005). Microhabitat requirements relating to geofeatures have also been linked to lizards (Michael et al. 2010; Ryberg et al. 2015). However, the scales of applicability and places within which these cross-taxa relationships with geofeatures hold, and how these translate into overall diversity relationships, remains unclear. The relevance of geofeatures

used in this way might make them more applicable to modelling species' distributions and abundances than overall biodiversity.

Further considerations and caveats of using geodiversity in ecology

Linking biogeomorphology and geodiversity

The biotic and abiotic environment affect one another in bidirectional, complex and often non-linear ways (Viles et al. 2008). The field of study aimed at analysing these complex interactions and specifically the effect of organisms on landscapes is biogeomorphology (Naylor et al. 2002; Darby 2010; Corenblit et al. 2011; Viles 1988). This field seems to have been neglected by those researching geodiversity to date, despite much relevant theory and application. Firstly, from an ecologist's point of view, such work will be informative, especially in relation to the finer-scale interactions that we are attempting to capture with geodiversity data. Secondly, it should encourage ecologists to be cautious because not only do landforms affect ecology, but individual organisms and communities can in turn affect geomorphological landforms and processes, thus potentially complicating the observed relationships (Osterkamp et al. 2012; Corenblit et al. 2011; Eichel et al. 2017). This latter point is generally seen as the central focus of biogeomorphology (Naylor et al. 2002; Darby 2010), which is perhaps why this this field has been somewhat overlooked by ecologists attempting to link patterns of life to geodiversity.

It is difficult to determine these interactions between organisms and landforms at times and there are likely to be fine-scale feedbacks that affect macroscopic patterns, and *vice versa* (Stallins 2006; Viles et al. 2008). Disentangling these interactions is likely to be of interest to both biogeomorphologists and ecologists alike. For example, shrubs can cause uneven snow distribution which affects cryoturbation-based features (e.g. hummocks) via differential frost heave, but the microtopography of the geofeatures affects local site conditions and thus the probability of species establishing and surviving (Hjort & Luoto 2009). Meanwhile, there are a number of case studies concerning rivers (e.g. Corenblit et al. 2015; Gurnell 2015) and glacial features (e.g. Eichel et al. 2016; Eichel et al. 2017) where vegetation has significant effects on the geofeature measured as part of a geodiversity study. As in Eichel et al. (2016), identifying 'biogeomorphic feedback windows' will be important going forwards so that we may understand geofeature-species interactions more fully in relation to how they affect our theorised links between geodiversity and patterns of life.

Conserving Nature's Stage (CNS)

Considering where climatic changes will be most pronounced is essential for conservation planning, given the expected changes in coming decades and centuries. The geographic spread of climatic change has been estimated by consideration of climate velocities. One study has predicted that recent climatic divergence, which is where temperature and precipitation changes are proceeding in opposite directions, has been particularly high in mountainous areas, for example (Ordonez et al. 2016a). This has implications for species tracking temperature and precipitation. Such species will be most benefitted by conservation strategies that aim to preserve geodiversity (Ordonez et al. 2016a; Albano 2015). This is the rationale behind the 'Conserving Nature's Stage' (CNS) approach (Beier et al. 2015; Lawler et al. 2015; Anderson & Ferree 2010). In other words, this 'coarse-filter strategy' aims to preserve landscapes with a greater environmental heterogeneity, which should allow for the maintenance of the greatest range of environmental conditions possible, thus benefitting overall biodiversity, even if the species composition changes through time.

These geodiverse landscapes may also allow space for evolution in the long-term, which has been demonstrated using datasets spanning the Quaternary (Gill et al. 2015). However, Gill et al. (2015) recognise the challenges of linking geodiverse locations to long-term ecological and evolutionary processes and highlight that there is uncertainty beyond 100,000 years. Temporal studies of biodiversity change in geodiverse areas in recent decades are also lacking, but recent work has suggested that the thermal variability offered by mountainous areas exceeds expected climate warming in coming decades (Lenoir et al. 2013), which may offer further support to the CNS approach. It would be informative, though, to have a greater array of studies across a range of geodiverse conditions to infer biodiversity change in more recent decades. This could inform the extent to which behavioural adaptions might come into play, as well as the longer-term processes of environmental filtering and evolution. Similarly, CNS was recently brought into question over the inherent assumption that climatic changes will affect environmental features more slowly than biological communities (Hunter & Nibbelink 2017). This study considered the fact that sea level rise might essentially erase geofeatures in certain environments (the study area was coastal Georgia, USA). The authors concluded that CNS is a viable strategy for the salt marshes studied, but that sea level rise should be considered more readily in conservation assessments using the CNS approach.

Overall, considering that mountainous areas may be able to preserve thermal variability that exceeds climate change (Lenoir et al. 2013), the supposed underestimation of climate change velocity in mountainous regions (Dobrowski & Parks 2016), and that temperature and precipitation are expected to diverge in many mountainous areas worldwide

(Ordonez et al. 2016a), the preservation of geodiverse areas seems to be a practical conservation approach, so that we may conserve as wide a variety of environmental conditions as possible that may help to mediate the impact of climatic changes. Towards better conservation planning, however, it would be wise to explicitly consider and improve our quantitative understanding of the direct and indirect influences of climate on geofeatures and, in turn, on theorised ecological processes. This necessitates further quantitative work across a range of environments and taxa, and using appropriate geodiversity measures.

The individual and inherent values of geodiversity and of biodiversity

The possibilities of the CNS approach are encouraging, but proponents, decision makers, and practitioners must be careful to not overlook the fact that geodiverse areas are not necessarily biodiverse, and biodiverse areas are not necessarily geodiverse (Fig. 2). Practically, conservation assessments need to be holistic (Matthews 2014). For example a conservation assessment that assumes a link between geodiversity and biodiversity may overlook relatively geohomogeneous areas (i.e. those lacking in geodiversity) that contain highly unique species, or even high biodiversity. Meanwhile, not all geodiverse areas will harbour high biodiversity, particularly if they are extreme (climactically or geologically). At the same time, conservation assessments focussed solely on biodiversity may miss opportunities for protecting unique geofeatures (and unique ecology-relevant processes therein), which may house distinctive species or be important for species into the future as the climate changes (Albano 2015), or simply be sites of special geoheritage value with no particular ecological relevance (Peña et al. 2016). Finally, CNS must continue to recognise the value of connectivity and biotic interactions, which are documented and discussed elsewhere as key considerations when using geodiversity in biodiversity conservation (Mcrae et al. 2017; Anderson et al. 2015; Urban et al. 2016). However, whilst biotic interactions can affect biodiversity–heterogeneity patterns (Wilson 2000), the role of abiotic factors is thought to dominate over biotic factors in the long term (Benton 2009).

	Relatively Biohomogeneous	Relatively Biohomogeneous, but with unique species	Relatively Biodiverse
Relatively Geohomogeneous	Desert dune fields	Savannah grasslands	Tropical lowlands
Relatively Geohomogeneous, but with unique geofeatures	Young volcanic landscapes	Wetlands	Karst landscapes
Relatively Geodiverse	Low altitude glacial and periglacial environments	High latitude mountain areas	Mountainous tropical forest

Figure 2 Comparing and contrasting diverse and homogeneous areas regarding biota and the abiotic environment, with examples. There is inevitably overlap between the categories and examples. Here, we are developing Matthews' Fig. 3 (2014; p. 62) by explicitly recognising unique geofeatures and ecosystems.

Data and techniques

Geomorphometry and remote sensing

Recent studies have demonstrated the application of geomorphic techniques in the context of geodiversity (Seijmonsbergen et al. 2014; Athanasios et al. 2016), with some explicitly relating these to biodiversity and conservation science (e.g. Theobald et al. 2015; Bailey et al. 2017). These techniques allow us to quantify the landscape like never before in a move that will add to existing, albeit relatively crude, landscape parameters. Novel geomorphometric data may also be less susceptible to multicollinearity with climatic variables than variables such as elevation, for example (Bailey et al. 2017). The increasing availability and specificity of digital elevation models (DEMs) will no doubt increase the ubiquity of these approaches goings forwards. However, we need to ensure that the quantified landscape remains ecologically meaningful and is linked to existing theories and known processes, including (but certainly not restricted to) those in Table 2. Remote sensing will also progress the field of geodiversity research. Data associated with remote sensing for geodiversity have been discussed elsewhere (e.g.: Hjort & Luoto 2012; Bailey et al. 2017), so are not covered in detail here. In terms of the state of the art, the combination of LiDAR and hyperspectral sensors has been proven in ecology (Eitel et al. 2016), but application of these techniques to the geophysical environment would no doubt also be beneficial. So too would the more extensive use of unmanned aerial vehicle (UAV) platforms, which have been demonstrated in geology (Fernández-lozano & Gutierrez-alonso 2016) and geomorphology (Bishop et al. 2012). Studies linking UAV-derived

land surface data to ecological patterns are limited. However, a recent study in glacier forelands provides a prime example of the potential of these techniques (Eichel et al. 2017).

In terms of hydrological features and moisture levels, these have often been assumed to be captured via DEM-based metrics, such as the topographic wetness index (TWI). TWI is strictly not in agreement with our definition of geodiversity, which requires the measurement of geofeatures, which are 'spatially explicit landforms, hydrological features, or land surfaces'. The exclusion of TWI from geodiversity has been done elsewhere (Tukiainen, Bailey, et al. 2017). Whilst slightly different versions exist, TWI essentially uses local topography to quantify runoff and theoretically relates to long-term moisture availability (Wilson & Gallant 2000). However, the choice of flow algorithm has been proven to have a considerable effect on TWI and subsequent relationships with ecological variables (Kopecký & Čížková 2010) and it therefore does not necessarily correlate well with the presence of actual hydrological features.

DEMs and remotely sensed data strongly relate to one of the original justifications for the use of geodiversity in biodiversity science and conservation, which is to do with cost effectiveness: geodiversity data may frequently be cheaper and faster to collect than species' occurrence data (Hjort & Luoto 2010). These data also provide consistent mapping of the environment over large areas, which is often infeasible in the field. Beyond this, the value of geodiversity data for enhancing our understanding of ecological patterns and processes and applying these to practical conservation planning efforts, regardless of cost and ease, must not be overlooked. With the open spatial data revolution (Kitchin 2014), our ability to quantify geodiversity and geofeatures should only move forwards.

Seeing earth science maps through the eye of an ecologist

Data relating to land surface materials (bedrock; parent material; soil), the relevance of which is assessed above, provide such an example of increased data availability. A prime example of these data is the 'SoilGrids1km' dataset (Hengl et al. 2014), which is 1 km^2 resolution 'global 3D soil information system'. This datasets maps the earth surface using ca. 110,000 soil profiles and contains information on pH, soil depth, texture, and many more soil parameters, all of which have been assessed with regards to their ecological relevance above (e.g. Augusto et al. 2017). The prospects of such a dataset are clearly extensive within the context of geodiversity–biodiversity research.

Despite this availability of data and the extensive sources of digitised geological maps, however, we would argue that use of existing geological and geomorphological maps is sub-optimal in ecology. The key point that we wish to make here is that geological metrics, whether relating to richness or coverage of a geological types, must be ecologically meaningful and

supported by ecological theory relating to minerals or nutrients, for example. For example, a high value for a geological richness metric might result simply from many types of rock that have very similar theorised links to ecology. In this case, we should not be counting these as separate geological types because the resulting metric is not fit for purpose from an ecological point of view, despite being of probable value to geoscientists in terms of understanding the earth's history. Greater collaborations here between ecologists and geoscientists would be advantageous, so that we may make geological maps more suited to our purposes. Such collaborations could help us use existing geological maps effectively in ecology and link rock age to physical processes and conditions such as weathering and slope angle, for example (Otto et al. 2016). The case remains the same for existing geomorphological maps: are all geomorphological features uniquely relevant, ecologically? If not, then they should not be included separately in geodiversity–biodiversity analyses and using broad landform classes (e.g. ridge; valley; hollow) might be preferable. Better consideration of these matters, the outcome of which will vary between study areas, should result in ecologically meaningful geodiversity components.

Measures of geodiversity and biodiversity

Whilst we consider there to be unique value in investigating geofeatures individually and considering their combined effect (as in Bailey et al. 2017), rather than using compound metrics (e.g. Albano 2015; metrics assessed in Table 1), we recognise their value. Indeed, there may be much to gain from producing geodiversity metrics in line with the biodiversity literature and testing them against one another. However, geodiversity metrics are under-explored, especially when paralleled to the sophistication of those in biodiversity (Magurran & McGill 2011; but see: Athanasios et al. 2016). We also have only a limited appreciation of relationships between biodiversity and geodiversity metrics beyond richness, which are themselves still far from fully established. For example, could geodiversity help to explain spatial beta diversity for a given taxonomic group? How comparable is beta diversity in geofeatures with beta diversity in plants or animals?

One example of where an aspect of biodiversity that goes slightly beyond raw richness has been considered, found that the spatial distribution of rarity-weighted richness (Albuquerque & Beier 2015) was slightly better explained when a geodiversity was considered (Tukiainen, Bailey, et al. 2017). However, this study still used a richness-based measure of geodiversity and it was only the biodiversity metric that went beyond richness. Building on this, similar analyses would be most revealing, but ones which also adjust the geodiversity measure. Therefore, we suggest a focused progression of geodiversity metrics in-line with

those already used in ecology: e.g. alpha, beta, and gamma diversity; species' distributions; species' traits and functional diversity; rarity-weighted richness (RWR); endemism; community composition (e.g. le Roux & Luoto 2014); Shannon–Weaver diversity (e.g. Albano 2015); and Simpson diversity. For example, one recent study calculated several geodiversity metrics (richness, as well as Shannon's and Simpson's diversity and evenness indices) that could be, but were not in this case, used within biodiversity modelling, for example (Athanasios et al. 2016). The purpose of this would be to better understand various aspects of patterns of life, as defined according to existing biodiversity metrics, in relation to various measures of geodiversity. The key point of consideration here, however, is that any metrics developed for geodiversity must be based on theory and applied deductively within ecology.

A possible workflow for ecologists using geodiversity and geofeatures

There is a lot to consider here for an ecologist who wishes to incorporate geodiversity and geofeatures into their research. We have therefore proposed a workflow (Fig. 3) which, when combined with the key questions outlined below, should make for an effective tool in advancing ecological research by incorporating geodiversity. Importantly, the approach focuses on the application of ecological theory that is relevant to a study's: geographic location; geodiversity metric/s; biodiversity metric/s; focal geofeatures; spatio-temporal scale/s; and taxonomic group/s. The conceptual workflow should be applicable to biodiversity and species distribution modelling.

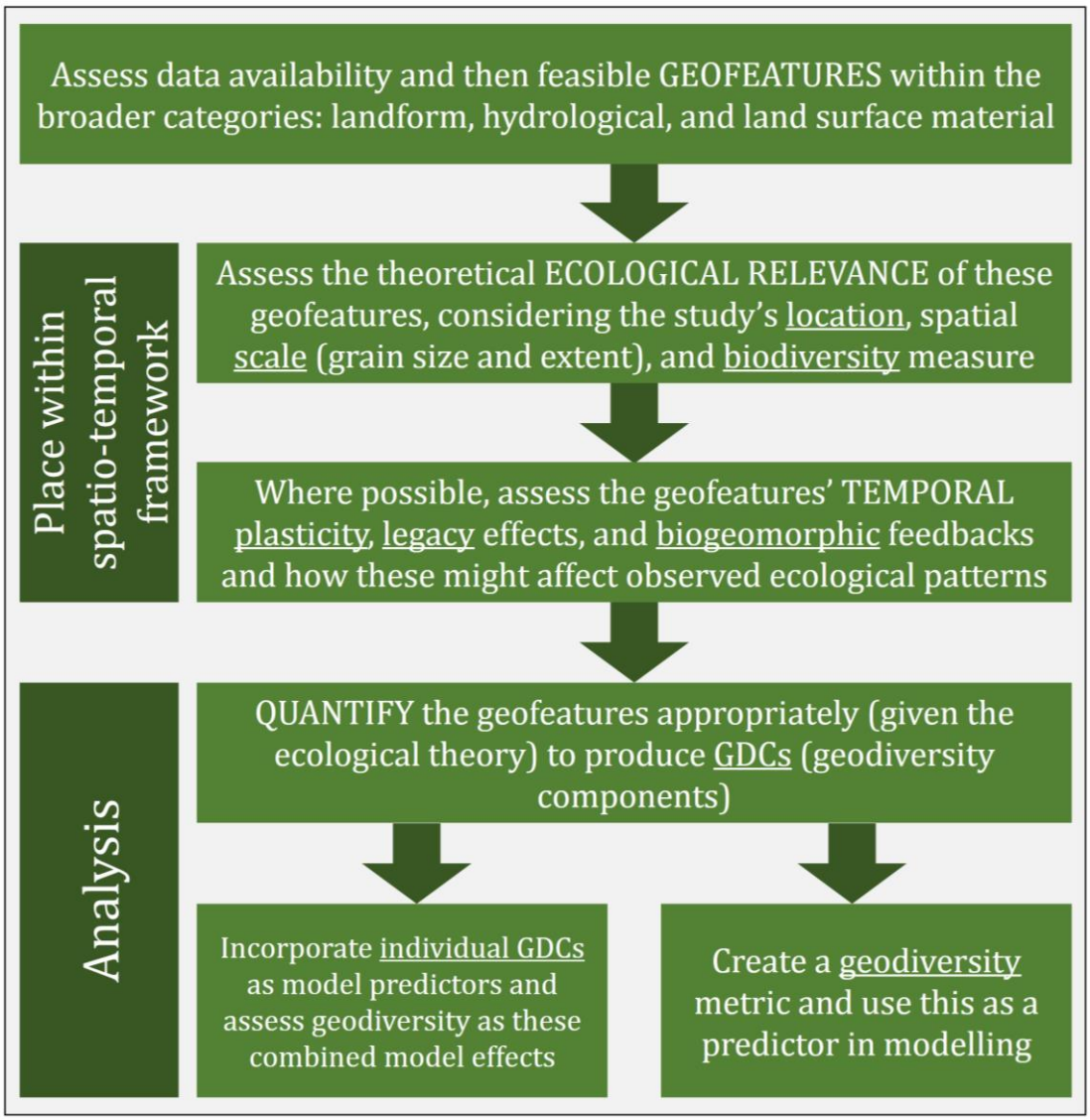


Figure 3 A proposed workflow for ecologists wishing to incorporate geodiversity and geofeatures into their research, especially when modelling biodiversity or species' distributions.

Seven key questions (most broad at the top)

1. Where is geodiversity most relevant taxonomically and geographically, and at what spatio-temporal scales across taxa and geographic space, for advancing our understanding of patterns of life? As well as terrestrial, anthropogenic, marine, and freshwater environments might also be considered.
2. Which facets of 'patterns of life' correspond most closely to different measures of geodiversity? These might include, but are not limited to: species richness; species' distributions; beta diversity; rarity-weighted richness (RWR). Comparable geodiversity metrics, based on explicit geofeatures, should be developed.

3. Where does the role of environmental heterogeneity (including geodiversity) peak in improving biodiversity models? Are extremely heterogeneous locations less diverse than those with intermediate heterogeneity?
4. To what extent can geodiversity and geofeatures inform our understanding of patterns in species' traits across spatial scales?
5. Can geodiversity help explain holes in species distributions?
6. Exactly how can geofeatures and geodiversity be used to improve ecological forecasting under climate change? This may extend to refugia.
7. Are automatically and semi-automatically derived geofeature data from digital elevation models (DEMs) better than expertly-mapped data in terms of how much they enhance our ecological modelling and how much they cost to produce (time and money).

Main conclusions

Geodiversity, and its constituent, explicitly defined geofeatures, represent an advancement of how we quantify heterogeneity for use in ecological research across scales. We have here aimed to advance this concept through a full assessment of geodiversity research in ecology to date, before discussing its prospects. We have done so through the *eye of an ecologist* with the intention of more fully integrating geodiversity, not born within ecology, into the discipline into a way that has not been done before: explicit consideration of established ecological theory; spatio-temporal scale; and taxonomic and geographic applicability. Our efforts were inspired by recent quantitative studies that have demonstrated the additive effect that geofeatures and geodiversity can have in relation to our ecological knowledge. These data seem to represent an important set of abiotic predictors once the climatic filter has been passed and geofeatures allow us to explicitly link ecological patterns to the geophysical landscape in a way that more widely-used heterogeneity metrics have not. Collaborations between ecologists, biogeomorphologists, geologists, and geomorphologists will be essential moving forwards but, together, these geodiversity data and collaborations should progress our ecological understanding and improve the ability of our models to predict biodiversity and species' distributions in space and time.

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Author contributions

Most authors (KR, JJB, ACS, WB, SF, EvL) attended an ideas workshop at Amsterdam University, (organised by KR), which generated the impetus and key foci for the manuscript. The content was then largely written by JJB, with significant inputs from KR, then DK = RF = ACS, then SF, then WB and EvL. FS contributed conceptually and practically in the later stages. DB contributed ideas throughout.

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PAPER II: MODELLING NATIVE AND ALIEN VASCULAR PLANT SPECIES RICHNESS: AT WHICH SCALES IS GEODIVERSITY MOST RELEVANT?

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Abstract

Aim To explore the scale-dependency of relationships between novel geodiversity measures and both native and alien vascular plant species richness.

Location Great Britain

Time period Data collected 1995-2015

Major taxa Vascular plants

Methods We calculated terrestrial native and alien vascular plant species richness (6,932 species in total) across the island of Great Britain at 1 km^2 (N=219,964) and 100 km^2 (N=2,121) grain sizes and regional extents 25-250 km in diameter, centred around each 100 km^2 cell. We compiled geodiversity data on landforms, soils, hydrological and geological features using existing national datasets, and used a newly developed geomorphometric method to extract landform coverage data (e.g. hollows, ridges, valleys, peaks). We used these as predictors of species richness, alongside climate, commonly used topographic metrics, land-cover variety and human population. We analysed species richness across scales using boosted regression tree (BRT) modelling and compared models with and without geodiversity data.

Results Geodiversity significantly improved models over and above widely used topographic metrics, particularly at smaller extents and the finer grain size, and slightly more so for native species richness. For each increase in extent, the contribution of climatic variables increased and that of geodiversity decreased. Of the geodiversity variables, automatically extracted landform data added the most explanatory power, but hydrology (rivers, lakes) and materials (soil, superficial deposits, geology) were also important.

Main conclusions Geodiversity improves our understanding of, and ability to model, the relationship between species richness and abiotic heterogeneity at multiple spatial scales by allowing us to get closer to the real-world physical processes that affect patterns of life. Greatest benefit comes from measuring the constituent parts of geodiversity separately, rather than one combined variable (as for most of the few studies to date). Automatically extracted landform data, the use of which is novel in ecology and biogeography, proved particularly valuable in our study.

Introduction

Understanding spatial patterns of biodiversity is important for scientific theory, conservation and management of ecosystem services (Lomolino et al. 2010; Hanski et al. 2012). Climatic variables are well known to correlate strongly with species richness over large spatial extents (Diniz-Filho et al. 2003); correlates of species richness at smaller extents (regional and landscape scales) are less well established (Field et al. 2009; Valdés et al. 2015), environmental heterogeneity is widely thought to be important (Stein et al. 2014; Stein 2015). Although a bewildering array of environmental heterogeneity measures has been used, there is growing interest in geodiversity, both as having value in itself (Gray 2013) and as a potential correlate and predictor of spatial biodiversity patterns (Lawler et al. 2015).

Geodiversity, which we define as 'the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms' (Fig. 1a), may be an important correlate of biodiversity at landscape and sub-national scales (Gray, 2013; Barthlott et al., 2007; Hjort et al., 2012; Lawler et al., 2015). Geodiversity comprises 'geofeatures' (Fig. 1b), which are the individual landforms and geological types (for example) that constitute the abiotic landscape. Quantification of these geofeatures varies across studies (e.g. Pellitero et al, 2015). We introduce the term 'geodiversity component' ('GDC'; Fig. 1b), to refer to the quantified geofeature, whether this be areal coverage (e.g. of a particular landform), richness (e.g. number of geological types), or length (e.g. a river). These GDCs together measure 'geodiversity' at the scale being studied. The GDCs we use here are intended to capture aspects of abiotic heterogeneity with which living organisms interact – and thus better and more explicitly measure environmental heterogeneity for the purposes of explaining species richness patterns than crude topographic measures such as mean slope, elevational range or mean aspect (Fig. 1). Such topographic measures have been widely used as correlates or predictors of species richness (Stein & Kreft, 2014), and to create a conceptual distinction we omit these from our definition of geodiversity.

A small but rapidly growing number of studies have found explicit geodiversity measures to add explanatory power to statistical models accounting for spatial biodiversity patterns (e.g. Pausas et al., 2003; Hjort et al., 2012; Kougioumoutzis & Tiniakou, 2014; Tukiainen et al., 2016; see review by Lawler et al., 2015). However, these studies have tended to either consider only one or two aspects of geodiversity or use a single geodiversity variable that simply counts geofeatures to produce an overall georichness measure (e.g. Hjort et al., 2012; Räsänen et al., 2016). The considerable improvements in explanatory power that these

preliminary approaches have achieved indicate the need for fuller analysis of the relationship between biodiversity and geodiversity, and particularly for explicit consideration of the separate components of geodiversity (Beier et al., 2015a). To date, very few studies have attempted this, and even fewer at geographic extents greater than the landscape scale, except for that by Tukiainen et al. (2016), which only analyses threatened species. Therefore, we now have evidence suggesting that geodiversity affects biodiversity, but our understanding of how it does so remains severely limited.

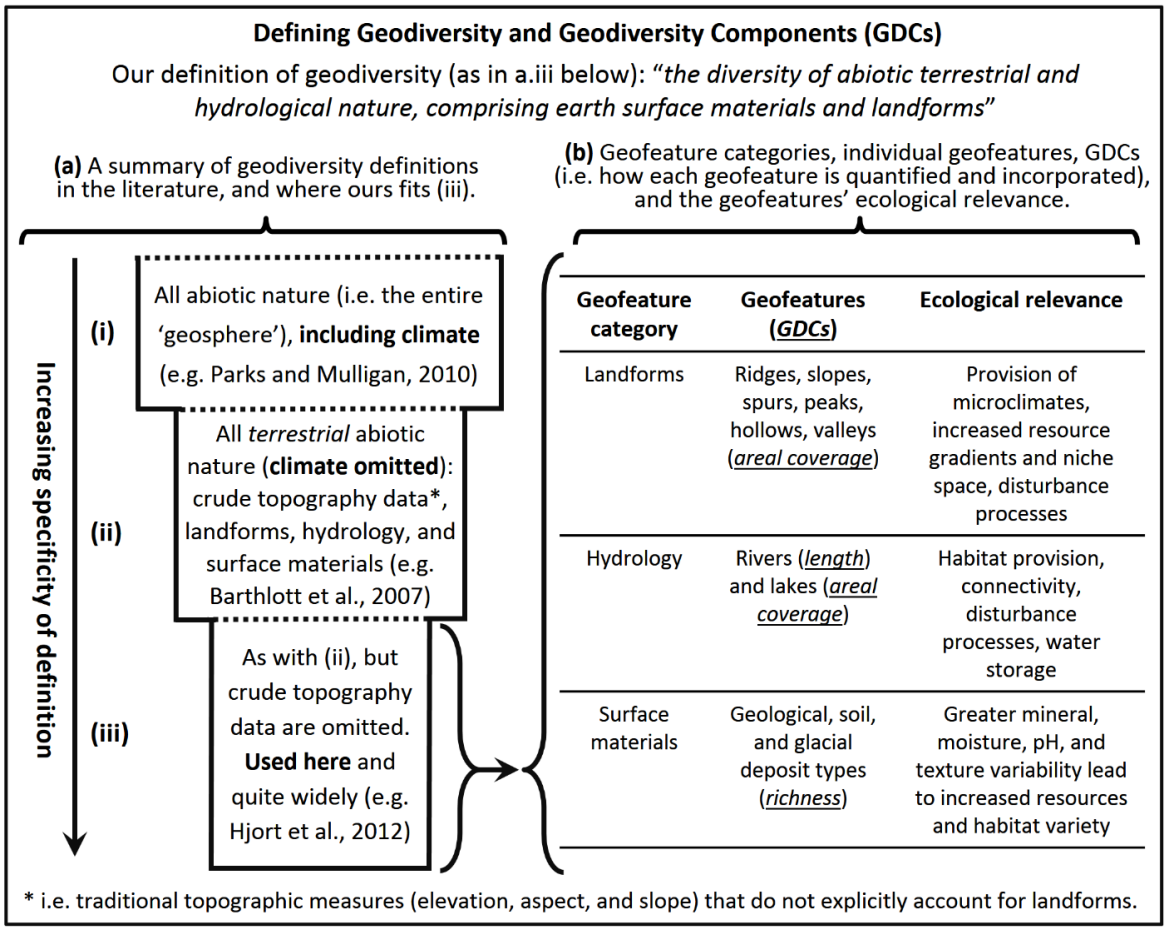


Figure 1 Our definition of 'geodiversity', which is among the more specific in the context of the wider literature. It omits relatively crude topography and climate data (a) and consists of geodiversity components (GDCs). The GDCs used in our study and their associated geofeatures and ecological relevance are listed (b).

All the GDCs in Fig. 1 measuring geomorphological, hydrological, geological and pedological geofeatures implicitly incorporate local abiotic variability and processes that are considered to have important influences on species richness via local resource availability, habitat diversity and niche variety (Burnett et al., 1998; Dufour et al., 2006; Bétard, 2013;

Albano, 2015; Hjort et al., 2015). Processes and abiotic variability related to geofeatures include, but are not limited to, microclimatic and sheltering effects around landforms (e.g. hollows and ridges); erosion, water storage capacity, physical and chemical weathering, pH variability, and mineral and textural variety via geology and soil; and water storage, transfer, and connectivity via hydrological features and rock composition and soil texture (Moser et al. 2005; Guitet et al., 2014; Hjort et al., 2015). GDCs may also be linked to natural geomorphological and hydrological disturbance processes, which are relevant to vegetation diversity and distributions (e.g. Viles et al., 2008; Randin et al., 2009; Virtanen et al., 2010; le Roux et al., 2013). Much of this information is lost when crude topographic measures, such as elevational range and mean slope, are used.

While we know much about the scale-dependence of the relationships between species richness and many of its commonly used correlates (Ricklefs, 1987; Rosenzweig, 1995; Mittelbach et al., 2001; Pausas et al., 2003; McGill, 2010), little is known about the scales at which richness correlates most strongly with geodiversity. Current thinking is that geodiversity is most relevant to species richness at landscape to regional extents, with climate dominating at broader (e.g. continental) extents, and biotic interactions more locally (Lawler et al., 2015). Theoretically, the local and landscape extents are most relevant because the various GDCs may be amongst the most variable predictors at this scale (Willis and Whittaker, 2002; Tukiainen et al., 2016), unlike climate. Therefore, if GDCs are important determinants of the spatial arrangement of biodiversity, we should expect their statistical explanatory power to be strongest at the local and landscape scales. We also know relatively little about the importance of grain size in modelling species richness. Theoretically, coarser grain sizes may average out fine-scale abiotic environmental heterogeneity over a larger area, thus relating more weakly to species richness, unless these fine-scale data are related to broad environmental gradients (Hawkins et al., 2003; Field et al., 2009).

A key reason for the limited research to date on geodiversity and its relationship with biodiversity is limited data availability. Especially in broad-scale macroecological studies, the widespread use of topographic measures to date, such as topographic range or standard deviation, in statistical models of species richness patterns, is explained primarily by the difficulty of obtaining more sophisticated and meaningful environmental heterogeneity variables (e.g. O'Brien et al., 2000). However, better data and processing capabilities now allow landscape heterogeneity to be quantified in new ways. Here we take advantage of these developments to move beyond simplistic topographic heterogeneity measures and derive novel geodiversity variables. In particular, we use 'geomorphon', a recently developed

geomorphometric tool for extracting landform data from digital elevation models (Jasiewicz & Stepinski, 2013). This allows low-cost quantification of landform features, which we use to measure landform richness at a spatial resolution of 25m across the whole island of Great Britain.

Alien and native species richness are likely to relate differently to the abiotic environment (Pyšek et al., 2005; Kumar et al., 2006), but little work has compared the relationship of alien and native species richness to environmental heterogeneity. Native species have had longer to equilibrate with abiotic environmental conditions (Räsänen et al., 2016), so their richness may be expected to be more closely related to geofeatures and topography. Conversely, geofeatures may account less well for alien species richness, especially of neophytes (species introduced after 1500 AD), which are more likely to be found where temperatures are higher and where there is greater human presence and connectivity via transport networks (Pyšek, 1998; Celesti-Grapow et al., 2006). An exception may be waterways; these geofeatures can promote the spread of alien species (Deutschewitz et al., 2003). Natural disturbance processes may also create suitable conditions for alien species (Fleishman et al., 2006). Broadly, we expect native species to have the strongest relationship with geodiversity, followed by archaeophytes (alien species introduced before 1500 AD) and then neophytes.

Overall, despite the clear potential of geodiversity for improving our understanding of spatial biodiversity patterns in relation to environmental heterogeneity, its incorporation into biodiversity modelling is underdeveloped conceptually, spatially and empirically. Outstanding questions include at what spatial scales and in which types of location is geodiversity most relevant? For which taxa? Does it relate differently to alien species than to native species? Which geofeatures are most important? Here, we begin to address some of these knowledge gaps by analyzing the relationships between a wide range of GDCs and the species richness of both native and alien vascular plant species richness across Great Britain. We test the degree to which GDCs add explanatory power over and above widely used topographic and climatic variables at varying spatial scales, using two grain sizes and either seven (small grain size) or five (large grain size) study-area extents. Our main aims are to determine: (i) the scales at which geodiversity best accounts for species richness patterns; (ii) which components of geodiversity account for the most variation in species richness, and how much; and (iii) whether geodiversity–species richness relationships differ between native and alien species. Specifically, we tackle to following hypotheses: (H_1) geodiversity will contribute significantly to biodiversity models, particularly at smaller study-area extents (Hjort et al., 2015; Tukiainen

et al., 2016); (H_2) the most relevant GDCs will vary between native and alien species (Deutschewitz et al., 2003) and, within alien species, between archaeophytes and neophytes.

Methods

Data

All predictors and predictor sets are summarised in Table 1. Data sources are detailed further in Appendix S1 in Supporting Information. Data were compiled for each 1km2 (N=222,111) and 100km2 (N=2,121) British National Grid cell using ArcGIS 10 (and GRASS GIS for geomorphometry, as detailed below) and processed and analysed in R (R Core Team, 2016).

Vegetation data were provided by the Botanical Society of Britain and Ireland (BSBI) via the Distribution Database at two grain sizes: 1x1km ('monad') and 10x10km ('hectad') grid cells corresponding to the British National Grid. The BSBI hosts a single database to which data are contributed by its volunteers and coordinators, who are strongly encouraged to use unbiased sampling (Walker et al., 2010). We used accepted data records (those verified within the database) collected between January 1995 and September 2015.

Species were defined as native, archaeophyte (probably introduced by humans pre-1500 AD), or neophyte (post-1500 AD). 'Casual aliens' (those that fail to establish) were excluded. Total (all three groups plus uncategorized species or those with no accepted status) and alien (archaeophytes plus neophytes) species richnesses were also modelled. Status definitions of each species followed the Wild Flower Society (2010), which, in turn, used multiple sources. Grid cells with less than 75% land coverage (considering lakes and ocean) were excluded. The final dataset contained 6,932 species: 1,490 natives, and 1,331 aliens comprising 151 archaeophytes and 1,180 neophytes, the rest of the species being unclassified.

Undersampled grid cells were excluded to remove bias arising from unrealistic species richness values because of undersampling. To determine undersampling, we performed a series of linear regressions that used climate and topography variables (not geodiversity) to account for species richness of grid cells within a 150 km radius around each hectad. A cell within this region was flagged as potentially undersampled if its standardized residual was less than -1.5 (i.e. if species richness in that cell was strongly over-predicted). This was repeated for every hectad, for both grain sizes. Grid cells flagged as undersampled more than 15% of the time they were analysed were classed as undersampled and removed. Two hectads (0.1%) and 2,147 monads (1%) were removed, leaving 2,121 and 219,964, respectively. This procedure

ensures that grid cells are not perceived to be undersampled when they are simply in harsh environments that would most likely contain few species anyway.

Table 1 A summary of the variables within each predictor set. The modelling uses three combinations of these predictor sets: (i) geodiversity only; (ii) all predictors except for geodiversity, and (iii) all predictors combined. Details of the data sources and URLs are provided (Appendix S1). *Bioclimatic variables (WorldClim): 1 (Annual Mean Temperature), 2 (Mean Diurnal Range (Mean of monthly (max temp - min temp))), 4 (Temperature Seasonality (standard deviation *100)), 6 (Min Temperature of Coldest Month), 12 (Annual Precipitation), 15 (Precipitation Seasonality (Coefficient of Variation)). References indicated by superscripts: [1]Jasiewicz and Stepinski (2013); [2]Intermap (www.intermap.com/data/nextmap); [3]NERC Earth Observation Data Centre (www.neodc.rl.ac.uk/); [4]Licence No. 2014/128 ED British Geological Survey © NERC. All rights reserved; [5]Ordnance Survey Strategi Data via Edina Digimap (http://digimap.edina.ac.uk/); [6]Corine Landcover (www.eea.europa.eu/publications/COR0-landcover); [7]Casweb (http://casweb.mimas.ac.uk/).

Predictor set	[sub-category] Variable	Resolution /scale	Measurement per 1x1km and 10x10km grid cell	Source (detailed in Appendix S1)
Geodiversity components (GDCs)	[Landforms] Areal landform: coverage of ridges, slopes, spurs, peaks, hollows, valleys.	25m (resampled from 5m)	Areal coverage r.geomorphon[1] in GRASS GIS 7.1.	NEXTMap data (Intermap, 2015[2] via NEODC, 2015[3])
	[Materials] Geological richness	1:50,000	Number of rock types	British Geological Survey[4]
	[Materials] Superficial deposit richness	1:50,000	Number of sup. dep. types	British Geological Survey[4]
	[Materials] Soil texture richness	1:50,000	Number of texture types	British Geological Survey[4]
	[Hydrology] River length	1:50,000	Total length	OS Strategi via Edina Digimap[5]
	[Hydrology] Lake area	1:50,000	Areal coverage	OS Strategi via Edina Digimap[5]
Climate	Bioclimatic variables*: 1, 2, 4, 6, 12, 15	30 arc-seconds (~1x1 km)	Mean	WorldClim (Hijmans et al., 2005)
Topography	Mean elevation; Standard deviation in elevation; Mean slope; Standard deviation in slope	25m (resampled from 5m)	Mean	NEXTMap data (Intermap, 2015[2] via NEODC, 2015[3])
Land cover and Anthropogenic	Land cover variety	100m	Number of land cover types	Corine Land Cover (2013)[6]
	2010 total human population	Census lower super output area	Total	2010 UK census data (Casweb)[7]

A 25x25m-resolution digital elevation model (DEM) was produced by resampling the 5x5m NEXTMap DEM from Intermap (obtained under academic license via the NERC Earth Observation Data Centre; see Table 1). Using the DEM, we performed geomorphometric

analyses (see below) and calculated commonly used topographic metrics (mean and standard deviation of elevation and slope). We downloaded ~1km^2 resolution climate data from WorldClim (Hijmans et al., 2005) and calculated land cover variety using the number of Corine land cover classes. Total human population per grid cell was calculated from 2010 census data from Casweb.

We compiled GDCs (Fig. 1b) using existing national datasets and automated extraction of landform coverage using geomorphometry (Table 1). Data included geological and superficial deposit diversity derived from 1:50,000 scale shapefiles provided by the British Geological Survey under an academic license. Soil texture data were from the same source but were 1km^2 resolution. We calculated river length and lake area using OS Strategi GIS data. We used the geomorphometric algorithm `r.geomorphon` developed by Jasiewicz & Stepinski (2013) in GRASS GIS 7.1 (GRASS Development Team, 2016) to automatically extract landform coverage data from the DEM (Appendix S2). The following landforms and features were mapped in raster format: peaks, ridges, shoulders, spurs, slopes, footslopes, hollows, valleys, flat areas and pits. We did not explicitly quantify mineralogy and pH, but these are implicitly incorporated via geology. Fossils, important for geoheritage and geoconservation (Thomas, 2012), were not included because of their limited theoretical relevance to the biodiversity patterns studied here, and lack of consistent data. Maps of climate, topography and geofeatures are presented in Appendix S3.

Analysis

We developed species richness models for three predictor sets: (i) geodiversity only, (ii) geodiversity variables excluded (leaving standard topographic variables, climate, population and land cover variety) and (iii) all variables. Models were run for all species groups (all species, native, alien, archaeophyte, neophyte) at twelve scales, where 'scale' refers to a unique combination of extent and grain size: seven geographic extents (whole of Great Britain ['national'] and 25, 50, 100, 150, 200 and 250 km diameter regions; see bottom of Fig. 2) and two grain sizes (1 km^2 [monad] and 100 km^2 [hectad]). The two smallest extents were not used for the coarser grain size for sample-size reasons. All regional models were run using the centroid of each hectad grid cell (n = 2,121) as the central point of each 'region'.

We used boosted regression trees (BRT) to model species richness in R 3.0.2 (R Core Team, 2016). BRT is a machine-learning method that can be seen as an advanced form of regression modelling (Elith et al., 2008). Here, with a complex dataset, largely unknown relationships (particularly GDCs) and multiple scales with variable collinearities and

interactions, using a BRT was efficient and appropriate. Additionally, BRT explicitly consider interactions, which can indicate important combined effects, and handle non-linearity and collinearity relatively well (Elith et al., 2008; Dormann et al., 2013). We also assessed collinearities separately, however.

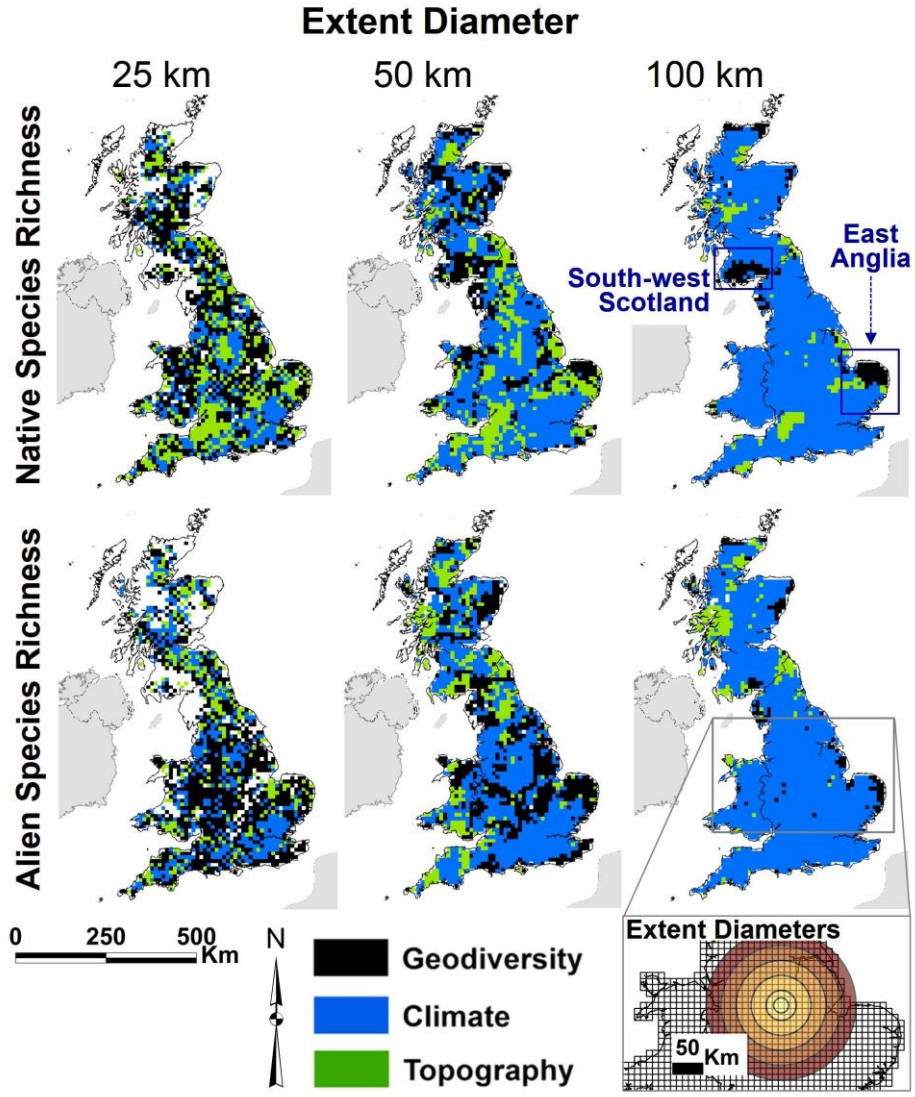


Figure 2 The dominant predictor set for native (top row) and alien (bottom row) species richness at the 1km^2 grain size for three spatial extents. White spaces are where data quantity was insufficient to run a reliable model or cells were excluded as they were undersampled. An example of the six extent diameters (25, 50, 100, 150, 200, and 250 km) is shown in the bottom-right, in this case for British National Grid cell SK54, which is one of 2,121 cells around which species richness was analysed at the two grain sizes and six extents.

We used `gbm.step` (`gbm 2.1.1` package in R; Ridgeway, 2015) to implement BRT. This function controls the number of terms, to produce parsimonious models. To quantify modelled effects of individual explanatory variables, the contribution (relative influence) of each predictor was obtained from `gbm.step`. These are scaled to add to 100, where '100' for

a predictor would mean that it contributed solely to the final model. Where the model contribution reflected a negative relationship with species richness, we then made the value negative for display purposes. Combined model contributions were calculated for the predictor sets and subsets defined in Table 1. We used a tree complexity of 3 (allowing up to three-way interactions; Elith et al., 2008), a bag fraction of 0.5, and a preferred learning rate of 0.05, which was occasionally reduced to 0.01, 0.005, and then 0.001 according to data requirements. Predictors contributing <10% (or sometimes <7.5%) were removed from the initial model, which was rerun with the simplified predictor set to produce the final results (further details in Appendix S4).

As well as evaluation using internal fit statistics ('self-statistics'), models were validated using 10-fold cross-validation (CV) in the GBM package. This approach randomly subsamples the data ten times according to the user-defined bag fraction; our bag fraction was 0.5, so each time 50% of the data were used to parameterize the model and the other 50% to evaluate it. The final cross-validation correlation statistic is the mean correlation between the training and testing data across ten runs. Model statistics were compared with and without GDCs using paired-samples t-tests.

Results

GDCs made the biggest contributions to models at the smallest study extent and the smallest grain size (in the geodiversity column of Fig. 3, the left-hand blue boxplot is the highest). At this scale, geodiversity was the strongest of all the predictor sets (of all the left-hand blue modelled contribution of geodiversity declined substantially relative to the other types of variable. GDCs were not relevant at the larger extents, giving way particularly to climate and human population. Climate was more important for archaeophytes than neophytes. The contribution of 'topography' (the coarse variables typically used in modelling species richness patterns) showed similar patterns to geodiversity, but was less important at smaller scales and declined less sharply as scales increased. Mapping the results (Fig. 2) shows the widespread dominance of the geodiversity predictor set at the smallest geographic extent, its

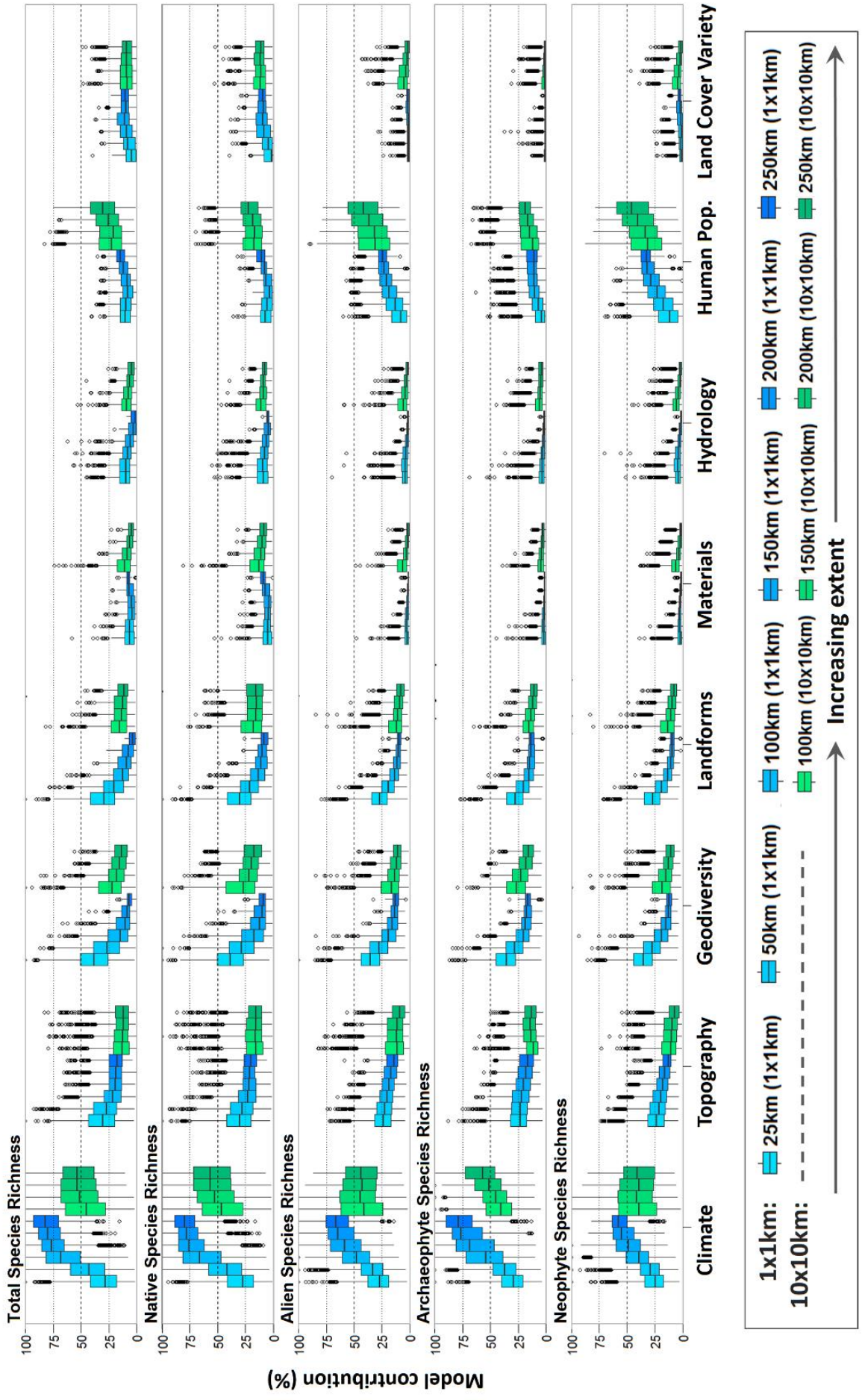

Total Species Richness
Native Species Richness
Alien Species Richness
Archaeophyte Species Richness
Neophyte Species Richness
Model contribution (%)
100
75
50
25
0
Climate
Topography
Geodiversity
Landforms
Materials
Hydrology
Human Pop.
Land Cover Variety
1x1km:
10x10km:
25km (1x1km)
50km (1x1km)
100km (1x1km)
150km (1x1km)
200km (1x1km)
250km (1x1km)
100km (10x10km)
150km (10x10km)
200km (10x10km)
250km (10x10km)
Increasing extent

Figure 3 (previous page) Combined model contributions (%) of each predictor set (climate, topography, geodiversity) and geodiversity subset, as well as isolated predictors human population and land cover variety. All scales are shown (except national): grain sizes (1x1km cells in blue, 10x10km in green) and extent diameters (lighter [further left] = smaller). A high resolution version of this figure is included (Appendix S5). This plot shows only model contributions of each predictor set, and gives no indication of directionality. 'Pop' = population.

Table 2 National extent results. Numbers show the combined model contributions (rounded to whole numbers) for each predictor set. Model evaluation (mean cross-validation correlation; CV) and fit statistics (self-statistics; SS) are also presented.

Grain size	Species Group	CV	SS	Dominant predictor (% model contribution)	Second highest predictor (% model contribution)	Third highest predictor (% model contribution)
1x1 km	All	0.376	0.380	Annual mean temperature (27%)	Precipitation seasonality (21%)	Min. temperature coldest month (15%)
	Native	0.366	0.369	Min. temperature coldest month (22%)	Annual mean temperature (20%)	Precipitation seasonality (16%)
	Alien	0.567	0.601	Human population (22%)	Annual mean temperature (17%)	Precipitation seasonality (14%)
	Arch.	0.541	0.569	Annual mean temperature (28%)	Mean Diurnal Range (16%)	Annual Precipitation (14%)
	Neo.	0.564	0.608	Human population (30%)	Precipitation seasonality (13%)	Annual Precipitation (11%)
10x10 km	All	0.717	0.737	Annual mean temperature (43%)	Human population (37%)	Mean Diurnal Range (6%)
	Native	0.659	0.696	Annual mean temperature (34%)	Human population (27%)	Mean Diurnal Range (10%)
	Alien	0.815	0.829	Human population (45%)	Annual mean temperature (40%)	Mean Diurnal Range (7%)
	Arch.	0.892	0.969	Annual mean temperature (43%)	Human population (13%)	Annual Precipitation (10%)
	Neo.	0.788	0.808	Human population (60%)	Annual mean temperature (24%)	Mean Diurnal Range (8%)

importance declining relative to climate with increasing extent, except in northern East Anglia and south-west Scotland where it persisted. At the national extent, climatic variables were dominant were dominant (Table 2), particularly annual mean temperature; human population was also often important, especially for neophyte species richness.

The contribution of geodiversity to biodiversity models was dominated by landform data from geomorphometry, but hydrology (rivers and lakes), and to a lesser extent materials (soil, superficial deposits and geology), were also important (Fig. 3; Appendix S5). Most trends

in specific GDCs followed that of geodiversity generally: declining model contribution with increasing scale. Model contributions from GDCs mostly resulted from positive relationships with biodiversity (Fig. 4; Appendix S6), but some relationships were negative. No GDCs were consistently negatively related to species richness. The highest positive model contributions for natives and aliens came from river length, valley coverage and lake area. Most GDCs were most strongly related to species richness at the smallest extent; the main exceptions were land surface materials, which, for native species, had highest contributions at the largest extent (Fig. 4).

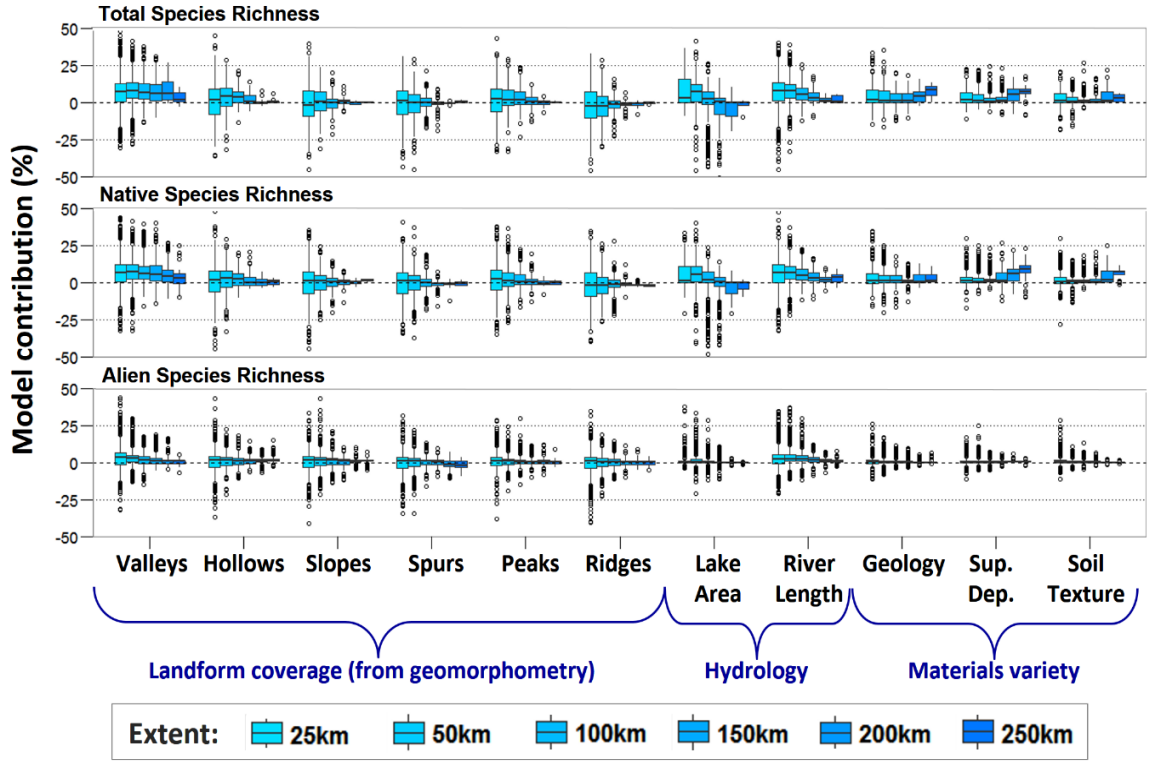


Figure 4 Model contributions from individual GDCs at the 1x1km grain size for each extent. These graphs are truncated at +50% and -50%, but only a small minority of points lie beyond these values. A full version of this figure with all species groups is included (Appendix S6). 'Sup. Dep.' = superficial deposits.

Across models accounting for species richness at all scales, interactions between GDCs and other predictors tended to be uncommon (Appendix S7), with the possible exception of precipitation and hollows for archaeophyte richness. The main interactions varied with scale but those between climate and topography, and between various climatic variables tended to be frequently dominant. Also, climate and mean elevation often interacted with human population, especially when modelling alien species richness. Collinearities between GDCs and topography and climate varied greatly across scales and between predictors (Appendices S8

and S9). Most GDCs were only weakly collinear with topography and climate (e.g. hydrology, rock variety, coverage of hollows, slopes and valleys) and others more strongly (e.g. coverage of peaks, ridges and spurs were moderately related to higher, cooler places at the coarser grain size and nationally), but these collinearities were still often much weaker than those between and within climate and topography predictors.

Self-statistics and cross-validation statistics were consistently higher (indicating better models) for larger extents, the coarser grain size of 100km^2, and alien species richness (Fig. 5; Appendices S10 and S11). Adding geodiversity often, but not always, resulted in significantly better models, especially at the smaller extents and for native species richness for both grain sizes (Table 3). Results for total species richness broadly followed those for native species richness (Fig. 3), despite the presence of many uncategorised species in the overall richness data. Results for alien species richness tended to follow those for archaeophytes, even though there were relatively few archaeophyte species.

[Discussion follows remaining Results figures]

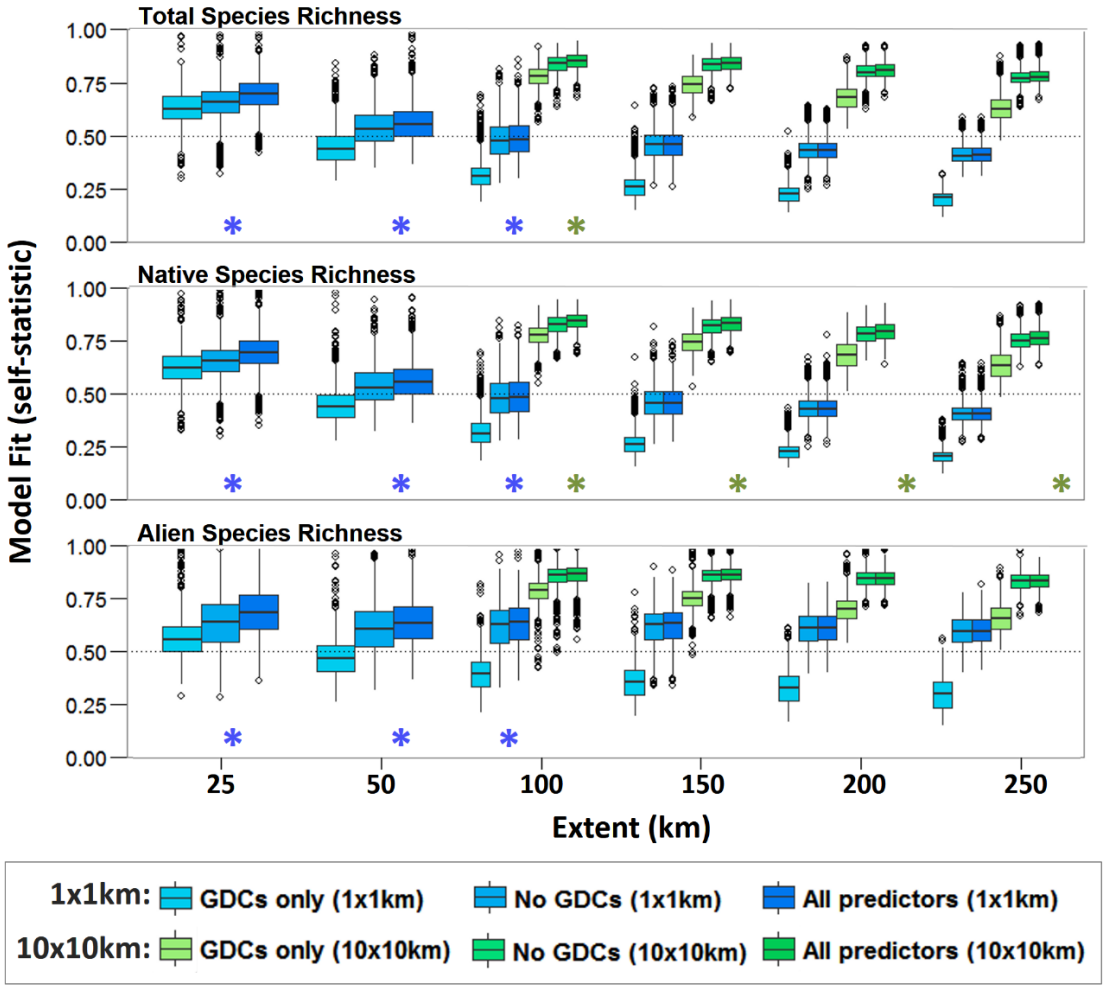


Figure 5 Comparison of model fit statistics (self-statistics; SS) with and without geodiversity according to grain size (colour/shade) and extent (x-axis).* = significant ($p < 0.01$, paired t-test) average model improvement across all models when comparing those without geodiversity (the middle boxplot for each scale) to those with all predictors (the right boxplot). Values are given in Table 3. Archaeophyte and neophyte results can be seen alongside these in Appendix S10, and an equivalent graph for cross-validation statistics is also provided (Appendix S11).

Table 3 Mean difference in model fit (self-statistics; SS) and evaluation (cross-validation; CV) statistics (also see Fig. 5 and Appendices S10 and S11) between models with and without geodiversity (i.e. a positive value indicates an increase in model performance after geodiversity was added). Shaded = significant average improvement ($p < 0.01$, paired t-test) in SS or CV across all models for that scale of at least 0.01. The 200km and 250km extents are not shown but continue the pattern of declining values in difference and worsening p value. The number of models compared is also shown.

Grain size	Species Group	25 km		50 km		100 km		150 km	
		SS	CV	SS	CV	SS	CV	SS	CV
1x1 km	All	0.039	0.018	0.022	0.007	0.008	0.004	0.001	0.001
		n = 1775		n = 2047		n = 2087		n = 2091	
	Native	0.041	0.015	0.023	0.007	0.008	0.003	0.002	0.001
		n = 1730		n = 2034		n = 2087		n = 2091	
	Alien	0.042	-0.006	0.029	-0.004	0.012	-0.001	0.005	0.001
		n = 1574		n = 2044		n = 2089		n = 2091	
	Arch.	0.039	-0.011	0.028	-0.003	0.014	0.000	0.007	0.001
		n = 1325		n = 1846		n = 2057		n = 2084	
	Neo.	0.038	-0.006	0.028	-0.003	0.011	-0.002	-0.001	-0.005
		n = 1588		n = 2042		n = 2089		n = 2091	
10x10 km	All					0.014	0.010	0.008	0.005
						n = 1697		n = 2037	
	Native					0.018	0.025	0.014	0.013
						n = 1697		n = 2037	
	Alien					0.006	-0.001	0.003	-0.004
						n = 1692		n = 2037	
	Arch.					0.021	-0.004	0.013	-0.003
						n = 1688		n = 2036	
	Neo.					0.008	-0.003	0.003	-0.004
						n = 1691		n = 2037	

Discussion

Geodiversity added significantly to models of vascular plant species richness, over and above widely-used topographic metrics, particularly at the smaller geographic extents (H_1). At the smallest extent, geodiversity contributed more than any other type of predictor accounting for species richness, while at larger extents climatic variables became increasingly dominant. With respect to individual geodiversity components (GDCs), of particular explanatory value were automatically extracted landform data, demonstrating that species richness–landform relationships can be detected at macroecological scales. These data represent a novel predictor set in macroecology and are relatively easily extracted from widely available DEMs. Our analyses also highlighted the importance of separately analysing individual GDCs, rather than lumping them into a single variable for use in biodiversity modelling, as done in most of the limited research to date. Results were broadly similar for alien and native species richness patterns (H_2), except that neophytes were more strongly related to human population than were the other plant groups. Results for total species richness were very similar to those for native species richness despite the presence of many uncategorised species in the overall richness data.

Geodiversity therefore succeeded in capturing unique dimensions of environmental heterogeneity that have theoretical mechanistic links to species richness, and which add explanatory power when modelling vascular plant species richness patterns (Stein at al., 2014). This is consistent with our first hypothesis (H_1), which was based on theorized links between biodiversity and the presence and diversity of both landforms and surface materials – reflecting the presence of more resources and greater habitat and niche variety (Moser et al. 2005; Anderson & Ferree, 2010; Hjort et al., 2012; Lawler et al., 2015), and possibly the results of some disturbance processes (le Roux et al., 2013). Also consistent with H_1 was the decline in magnitude of the geodiversity contribution with increasing extent, at both grain sizes, as other variables (particularly broad-scale climate) took over. Geodiversity therefore seems to provide a predictor set that can account for the variety of the abiotic environment at these finer extents ('landscape' scale), where broad-scale climate is more constant. At these scales, geodiversity data may be strongly related to microclimate and localised hydrological, edaphic and geological conditions that are relevant to species' establishment and persistence.

Theoretically, variables measuring fine-resolution environmental heterogeneity may contribute relatively little to models of species richness using large grain sizes because of the tendency for the heterogeneity to average out within grid cells (Field et al., 2009). If so, GDCs

such as those measuring landforms should reduce in explanatory power at larger grain sizes, when extent is held constant, while climate and productivity-related variables may increase. However, for the 100, 150, 200 and 250 km geographic extents (for which both grain sizes were assessed), we observed similar geodiversity results for each grain size, with often slightly higher relative geodiversity contributions at 100km^2 grain than 1km^2. This suggests that the size (extent) of the study area more strongly affects the relative contribution of geodiversity as a biodiversity predictor than does grain size. This may be because the heterogeneity measured by GDCs is correlated with broader environmental gradients, so the averaging of fine-scale variation at larger grains does not affect the explanatory power of GDCs much, compared with the large increases in the degree to which broad climatic and topographic gradients are captured at larger geographic extents (Hawkins et al., 2003). Further research is required on this question.

The general lack of strong and frequent collinearities and interactions between most GDCs and both topography and climate in our models suggests largely unique model contributions from geodiversity variables. While crude topographic variables such as mean elevation, elevational range and mean slope can provide useful information, as they did herein and in much previous research (e.g. Field et al., 2009; Hjort et al., 2012), these variables are typically strongly collinear with each other and with climate (e.g. Ferrer-Castán & Vetaas, 2005; Keppel et al., 2016; Appendices S8 and S9). More detailed analyses are needed of how GDCs correlate with other predictors in different places and at different scales. However, if using GDCs results in greatly reduced multicollinearity problems compared with using crude topographic variables, then our ability to determine cause and effect should be improved; this is consistent with the notion that GDCs relate more directly to mechanisms than do crude topographic variables (Gray, 2013; and see Introduction). That is, explicit consideration of landscape features in biodiversity modelling may enhance ecological understanding (Hjort et al., 2015), and is also likely to be highly relevant to modelling individual species' distributions.

Specific GDCs were important in the species richness models, consistent with the notion that species richness–GDC relationships can be detected at macroecological scales, and add to biodiversity models. These results were far more informative than using a compound measure of geodiversity. For example, we observed some negative relationships between biodiversity and various GDCs (Fig. 4), while valley coverage, river length and surface materials had more consistently positive model contributions. Modelled interactions between valley coverage and river length were not frequent or strong, and it is likely that the valley landform data detected smaller geofeatures (e.g. different erosional and depositional features produced

by geomorphological processes) that are ecologically important (Hjort et al., 2015) but not represented in the relatively coarse rivers maps that are generally available, and used in this study. Knowledge of surface (soil and superficial deposits) and sub-surface (geology) material richness was less useful than expected from previous research (e.g. Anderson and Ferree, 2010; Tukiainen et al., 2016). Perhaps explicitly considering the coverage of specific types of rock and soil (and mineralogy more generally) would be revealing. Further research on this would help us to better understand the links between specific GDCs and biodiversity.

The relative contributions of different predictors to alien and native species richness models showed broadly similar patterns across scales, but the magnitudes varied somewhat. The contributions from GDCs, particularly landforms, were greater for native species richness than alien, and native biodiversity models were also most improved by the addition of GDCs (partly consistent with H_2). Contributions from GDCs might therefore particularly add important information to native biodiversity models, which sometimes underperform compared to alien species richness models (Deutschewitz et al., 2003; Kumar et al., 2006). This finding is supported by the relative importance of geodiversity in explaining native richness compared to total richness models seen elsewhere (Räsänen et al., 2016).

The main difference between models of alien and native plant species richness lay in the contribution from human population, which was highest for neophytes, then archaeophytes, and relatively low for natives. While the relationship between alien species richness and cities or human populations has been known for some time (e.g. Pyšek, 1998; Deutschewitz et al., 2003; Kühn et al.,2004; McKinney, 2008), our results suggest that this relationship is more pronounced for neophytes and that the strength of this relationship is affected by scale (both extent and grain size). In line with known links between riverine habitats and neophyte species richness (Deutschewitz et al., 2003), we observed a substantial contribution of river length to neophyte richness models, and frequent interactions between river length and human population, implying increased human influence along rivers, which in turn may promote neophyte species richness. However, there was no notable relationship between native richness and river length, contrasting with findings elsewhere (Deutschewitz et al., 2003). Other aspects of hydrology (including lake area) tended to be less important in our models than landforms, topography, human population and climate. Overall, transport, for which human population provides a proxy, and river networks (and their interaction) could be promoting alien species' dispersal and thus increasing neophyte species richness (Hulme, 2009; Pyšek et al., 2010).

Geodiversity in biodiversity science and conservation

We have used geodiversity to try to provide more explicit representation of environmental heterogeneity than crude topographic variables. Indeed, GDCs more directly measure environmental conditions and processes, such as habitat diversity, resource gradients, and microclimatic and sheltering effects (Matthews, 2014; Hjort et al., 2015), thus enabling us to capture causal processes behind the biodiversity patterns more precisely. With this in mind, geodiversity may have benefits beyond species richness modelling – in species distribution modelling, for example. Investigating where geodiversity is most relevant to patterns of life globally requires research on geodiversity in geographic domains beyond our study area. It has also been suggested that such information might be important in the context of refugia by identifying parts of the landscape that can withstand long-term environmental change by providing stable microclimates (Keppel et al., 2015; Lawler et al., 2015); and geodiverse locations may facilitate species' adaptation to climate change, as well as their persistence (Albano, 2015; Maclean et al., 2015).

There are also practical reasons for improving our understanding of the relationship between geodiversity and biodiversity, the first relating to conservation. The idea known as 'conserving nature's stage' is gaining momentum (see Anderson & Ferree, 2010; Beier et al., 2015b). This suggests that, instead of targeting individual species and habitats for conservation, we target areas capable of supporting high biodiversity under future environmental changes, by either better maintaining the existing environment or by providing a greater environmental heterogeneity. Furthermore, geodiversity has been related to the diversity of threatened species richness and rarity-weighted richness, at least in high latitudes (Tukiainen et al., 2016). Indeed, the geodiversity data used in our study are likely to enhance our understanding of previously demonstrated links between abiotic diversity and site complementarity, which may be a more conservation-relevant biodiversity measure than raw species richness (Albuquerque & Beier 2015; Beier & Albuquerque). Areas high in geodiversity are also thought to promote greater resilience to climatic changes for biodiversity and for essential provisioning, regulating, cultural and supporting ecosystem services (Brazier et al., 2012; Gordon & Barron, 2013). However, we stress the importance of not overlooking the value of individual species in 'geohomogeneous' (low geodiversity) places, or unique geofeatures in species-poor areas. For example, an endangered species in a forest underlain by a single geology and few landforms should not be overlooked, whilst unique and irreplaceable geofeatures (e.g. certain fossils or rare geological units and mineralogy) will not always be relevant to biodiversity and present-day species' distributions, but have geoheritage value.

Another practical advantage of geodiversity data is that they are usually cheaper and faster to collect and collate than species' occurrence data (Hjort & Luoto, 2010) and, in areas where geodiversity correlates very strongly with biodiversity (e.g. northern Finland; Hjort et al., 2012), geodiversity may represent a useful surrogate for biodiversity. We have compiled a lengthy (but not exhaustive) table of GDC categories, including geology, soil, landforms and hydrology (Appendix S12) and a list of the remotely sensed datasets required, which may be a useful resource for reference. Importantly, a key dataset in our research was the automatically extracted landform data, which only required open-source GIS software (GRASS), a freely available algorithm within that software (r.geomorphon; Jasiewicz & Stepinski, 2013) and a DEM. Datasets related to land surface materials are less accessible in much of the world, but high resolution datasets of ecologically-relevant soil variables have recently become widely available (Hengl et al., 2014 or: www.isric.org/content/soilgrids). Other geodiversity data not used in our study might improve models further, including explicit data on pH and mineralogy, for example, or topographic wetness or insolation. Additional sources of geodiversity data, appropriate for smaller study areas than in our study, include those captured on airborne platforms: Hjort & Luoto (2010) used aerial photography combined with field surveys. It would be interesting to know whether such intensive data add explanatory power and ecological meaning to data obtained automatically from geomorphometry. Future sources of such data could include capture by Unmanned Aerial Vehicles (UAVs), release of archival data and increased data sharing on capture (Lowman & Voirin, 2016).

In conclusion, we have shown that geodiversity can add significantly to models of vascular plants, over and above widely used topographic metrics in our study area. We found some differences in the response of alien and native species richness to geodiversity; further research on this may be beneficial for conservation and management. Our findings demonstrate the largely unexploited potential of explicit geodiversity data, which may aid explanation by more directly measuring causal factors and reducing multicollinearity of explanatory variables. Research on the role of geodiversity across a variety of taxonomic and geographic domains is still in its infancy, and we have pointed towards some research needs. Our finding that automatically extracted landform data were valuable should encourage collaboration between geomorphologists, ecologists and biogeographers.

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Supporting Information

S1: Details of data sources in Table 1
S2: Geomorphometry Details
S3: Climate, topography, geodiversity, and geofeature maps
S4: Details of BRT modelling simplification
S5: High resolution version of Fig. 3
S6: Full version of Fig. 4 (individual GDC contributions for each species group)
S7: Model interactions summary
S8:.Collinearity summary across scales
S9: National extent correlation matrices
S10: Full version of Fig. 5 (model fit statistics; self-statistics)
S11: Model evaluation statistics (CV)
S12: Remote sensing of GDCs

Biosketch

Joseph J. Bailey is PhD candidate at the University of Nottingham, funded by the United Kingdom's National Environment Research Council (NERC; Studentship 1365737) and

supervised by RF and DB. His PhD comprises multiple individual projects across a number of scales and geographic locations. The common theme is the scrutinisation of when and where we can most effectively use geodiversity in modelling biodiversity and species' distributions.

Author Contributions

All authors contributed to the development of ideas for this research. JJB gathered and processed the data and conducted the analyses. JJB, RF and DB wrote the manuscript, with input from JH, and CL.

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PAPER III: CONSERVING NATURE'S STAGE? COMBINING GEODIVERSITY WITH CLIMATE AND TOPOGRAPHY TO ACCOUNT FOR THREATENED SPECIES DIVERSITY AND RARITY-WEIGHTED RICHNESS IN FINLAND

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Abstract

Improved understanding of threatened species diversity is important for long-term conservation planning and natural area management, especially under ongoing global change. Geodiversity – the diversity of earth surface materials, forms and processes – may be a useful biodiversity surrogate for conservation planning, as well as having conservation value itself. Links between geodiversity and species richness have been demonstrated; establishing whether geodiversity also relates to threatened species' diversity and distribution patterns is a logical next step for conservation biology. We used four geodiversity variables (rock type richness, soil type richness, geomorphological diversity, hydrological diversity), in addition to four climatic and topographic variables, to account for threatened species diversity across 31 of Finland's national parks. We also analyzed rarity-weighted richness (a measure of site complementarity) of threatened vascular plants, fungi, bryophytes, and all species combined. Our 1km^2-resolution dataset included 271 threatened species from 16 major taxa. We modeled threatened species richness (raw and rarity-weighted) using boosted regression trees. Commonly used climatic variables, especially the annual temperature sum above 5°C, dominated our models, consistent with the critical role of temperature in this boreal environment. Importantly, geodiversity added significant explanatory power, improving our understanding of threatened species. Greater geodiversity was consistently associated with increased threatened species richness across taxa; the combined effect of geodiversity variables was greater still in the rarity-weighted richness analyses (except for fungi). Geodiversity measures correlated most strongly with species richness (raw and rarity-weighted) of threatened vascular plants and bryophytes; such correlations were weakest for molluscs, lichens, and mammals. While it is well known that simple measures of topography improve biodiversity modeling and conservation practice, our results suggest that geodiversity data relating to geology, landforms, and hydrology are also worth including. This reinforces recent arguments that 'conserving Nature's stage' is an important principle in conservation.

Introduction

Land-use and climate change threaten species globally (Mantyka-Pringle et al. 2015). It is therefore increasingly important to understand and conserve species' diversity and distributions. One coarse-filter strategy in conservation and protected area management is that of 'conserving Nature's stage' (CNS), which centers on the physical structures that underlie biotic processes, while also recognizing that geodiversity – the diversity of earth surface forms, materials and processes (Gray 2013) – has conservation value in its own right (Anderson & Ferree 2010; Lawler et al. 2015). The CNS approach recognizes that geodiversity is related to biodiversity, suggesting that geodiversity should be incorporated into biodiversity research and conservation (Lawler et al. 2015). In practical terms, geodiversity data are frequently easier and less expensive to obtain than biodiversity data (Hjort et al. 2012), while advancing our scientific understanding of the spatial distribution of biodiversity is important for long-term conservation planning.

Well-mapped abiotic data are commonly used, together with data from ecological communities, to model or predict biodiversity for conservation planning (Brooks et al. 2004). Numerous studies have explored how abiotic factors are related to species' diversity and distributions (Anderson et al. 2015), and the relationship between environmental heterogeneity and species richness has been established across multiple taxa and spatial scales (Stein et al. 2014). Several studies have shown that local, idiosyncratic features, such as rock type, and landscape-scale factors, such as energy-related climatological variables, correlate with threatened species' patterns at different spatial scales, varying among taxonomic groups (Berg et al. 2002; Kreft & Jetz 2007; Lawler et al. 2015). Vascular plants are commonly studied and typically have strong relationships with climatic variables and topographic heterogeneity (Field et al. 2009), whereas the effect of abiotic conditions is less known for rare species in other taxonomic groups (e.g. Virkkala et al. 2005; Anderson & Ferree 2010).

Geodiversity represents a more complete characterization of earth-surface heterogeneity than topographic heterogeneity does. Here, we define geodiversity as distinct from widely used topographic measures such as elevation, range in elevation, and slope (herein referred to as 'topography'). Geodiversity includes explicit geofeatures such as rock types, soil types, geomorphological landforms and hydrological features. These can be explicitly incorporated into analyses, thus capturing aspects of local heterogeneity, such as microclimatic effects and microsite patterns, which are ecologically important, but are not captured by widely used climatic and topographic data (Field et al. 2009; Dobrowski 2011). Such local

heterogeneity, caused by geology, landforms and hydrology, relates to extended local resource gradients, niche space, and habitat variety (Stein et al. 2014).

Conservation biologists have rarely incorporated geodiversity into conservation prioritization efforts (Beier et al. 2015). However, geodiversity–biodiversity relationships are being increasingly demonstrated (Lawler et al. 2015) and may have considerable implications for conservation science. A significant link between overall plant species richness (dominated by common species) and overall geodiversity has previously been found (Nichols et al. 1998; Hjort et al. 2012). Establishing whether such a relationship exists between geodiversity and threatened species' diversity and distribution patterns is a logical next step for conservation biology. Indeed, quantifying geodiversity may provide greater insight into a landscape's potential to preserve species diversity (Anderson & Ferree 2010; Lawler et al. 2015).

However, numbers of species, and even numbers of threatened species, may not provide optimal measures by which to prioritize sites for conservation (Kirkpatrick 1983; Albuquerque & Beier 2015a). For optimal planning, managers often want to identify groups of sites that collectively represent multiple conservation targets (typically threatened species) in small areas (Albuquerque & Beier 2015a). Thus, instead of selecting the sites with the greatest species richness, or the most threatened species, a set of sites whose species assemblages complement each other and collectively capture the largest number of species is chosen (Albuquerque & Beier 2015b). Various site prioritization methods have been developed; software like Zonation (Moilanen et al. 2014) and Marxan (Ardron et al. 2010) are quite commonly used. However, a simpler alternative, rarity-weighted richness (RWR), has been shown to be efficient and reliable, allowing identification of priority sites (Albuquerque & Beier 2015b). Moreover, Albuquerque and Beier (2015a,c) recently demonstrated that site complementarity can be highly predictable from abiotic characteristics.

Here, we model the relationship between the physical environment and both threatened species richness and RWR at 1km^2 grain size across 31 protected areas of Finland. We use two predictor categories: (i) climate and topography (i.e. conventional predictors), and (ii) geodiversity. Our main aim is to determine the explanatory power of the geodiversity measures, which in this study are georichness variables. We expect data on geomorphology, geology, and hydrology to be relevant for landscape-scale patterns of threatened species richness and RWR because they should represent local geophysical conditions known to be important for the establishment and persistence of threatened species (Rich & Weiss, 1991; Engler et al., 2004). In theory, more threatened species should be able to persist where there is greater geological variety because of the broader variety of nutrients, resources, and pH (as

previously observed for common species; Hjort et al. 2012). Our study area only includes protected areas, so the levels of human impact are consistently low.

We analyze data for threatened species of vascular plants, fungi, lichens, beetles (Coleoptera), bryophytes, butterflies and moths (Lepidoptera), molluscs, mammals, and all of these combined. We use threatened species richness and RWR as measures of threatened species diversity and rarity, respectively. We (1) test the explanatory power of environmental variables in modeling diversity and RWR, (2) assess the consistency of these relationships across different taxonomic groups, and (3) study which georichness measures (rock type richness, soil type richness, geomorphological diversity, and hydrological diversity) add explanatory power to our models. We address the following four hypotheses, which are not mutually exclusive:

> H1: Threatened species diversity is strongly related to climate, and in high-latitude environments especially to energy-related climate variables (Hawkins et al. 2003; Stein et al. 2014).
>
> H2: Different taxonomic groups show different responses to climatic, topographic and geodiversity predictors (Stein et al. 2014).
>
> H3: Geodiversity measures improve models for threatened species diversity and RWR (Burnett et al. 1998; Anderson & Ferree 2010).
>
> H4: Threatened species diversity and RWR can be successfully modeled with climate, topography and geodiversity variables (Pausas et al. 2003; Hjort et al. 2012; Albuquerque & Beier 2015a).

Methods

Study area

The study area covers 31 national parks (Fig. 1) extending from southern Finland's coastal archipelago to glacially rounded hills with arctic-alpine conditions in the north. The parks vary from 6km^2 (Petkeljärvi) to 2850km2 (Lemmenjoki), covering 8091km^2 in total. Finnish national parks follow the definitions and management objectives of the International Union for the Conservation of Nature (IUCN) and Natural Resources Protected Area Management Category II (Heinonen 2013). We superimposed a regular system of 1km^2 grid cells and retained all cells containing threatened species records and with at least 10% of their area in a national park. For cells without threatened species records, we retained all cells located

entirely within national park boundaries. We therefore selected 6571 grid cells, 583 with observations of threatened species and 5988 without.

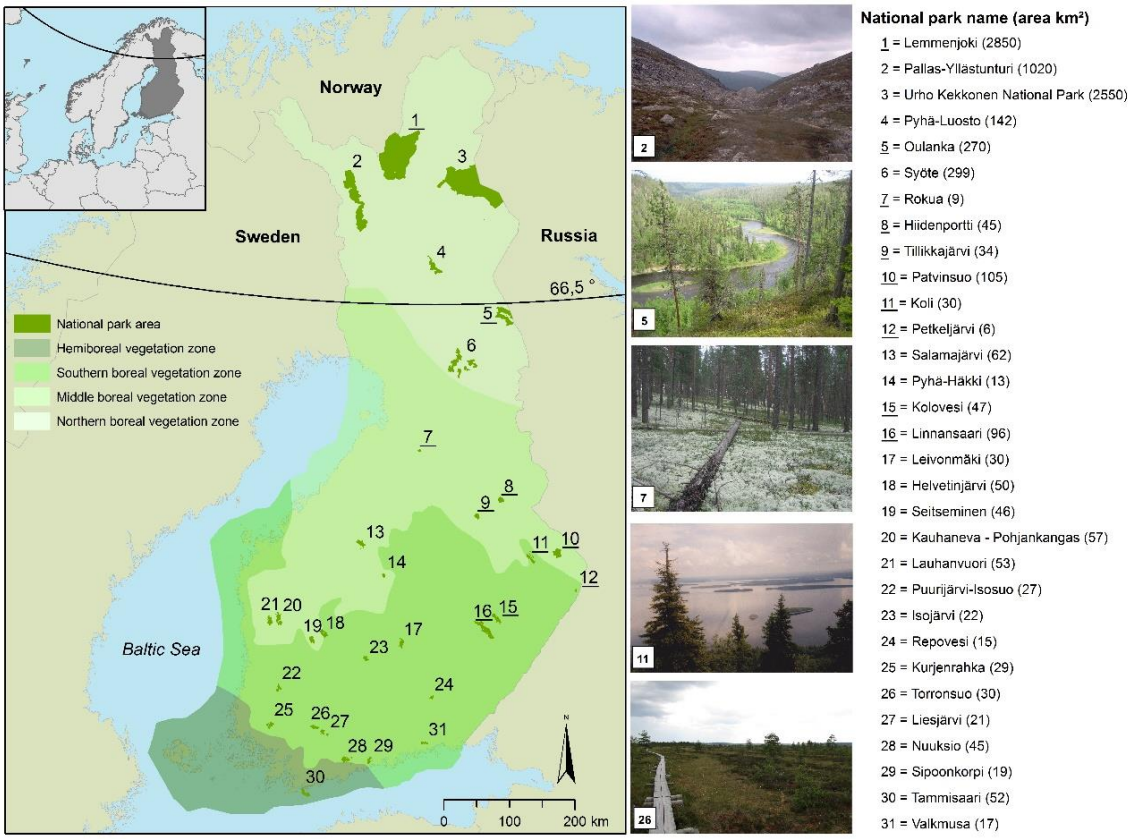


Figure 1. Locations of the Finnish national parks included in the study and major vegetation zones. As described in Analysis -section, national parks are split into 'east' and 'west'. The numbers for eastern parks are underlined.

Biogeographically, the study area covers hemi-, southern-, middle- and northern-boreal vegetation zones (Ahti et al. 1968) and includes a great variety of habitats, such as forests, fell areas and wetlands. Mean annual air temperature varies from −2°C in the north to approximately 6°C in the south (Pirinen et al. 2012), and the thermal growing season length (>5°C daily mean temperatures) from over 185 days in the south to less than 125 days in the north. Mean annual precipitation is moderate through all seasons and ranges between 444 and 739 mm (Pirinen et al. 2012; Table 1). Geologically, Finland is part of the Precambrian bedrock block of northern and eastern Europe, consisting mainly of crystalline rocks (Atlas of Finland 1990). The soils of Finland originate mainly from during or after the last glacial period and are dominated by ground moraine and peat depositions.

Table 1 The details of potential environmental variables compiled for boosted regression trees analysis (n=6571), of which a total of 8 variables, indicated with *, were selected, based on correlation analysis (see Methods section for further details).

Environmental variable	Unit	Median [min to max]	Source	Abbre-viation
GEODIVERSITY				
Rock type richness*	Number of rock types	1 [1 to 6]	GSF[a]	Rock rich
Soil type richness*	Number of soil types	2 [1 to 5]	GSF	Soil rich
Geomorphological richness*	Number of geomorphological feature types	6 [0 to 13]	GAM[c]	GM rich
Hydrological richness*	Number of hydrological feature types	1 [0 to 6]	NLS[b]	Hydro rich
CLIMATE				
Mean annual air temperature	°C	-1.1 [-2 to 5.9]	FMI[d]	
Growing degree days (>5°C)*	degree-days	639 [500.3 to 1448.3]	FMI	GDD
Mean temperature of coldest month (January)	°C	-13.4 [-14.5 to -3]	FMI	
Mean temperature of warmest month (July)	°C	13.1 [12.5 to 17.7]	FMI	
Seasonality (mean temperature of July – Jan)	°C	26.4 [20.1 to 29.3]	FMI	
Mean annual precipitation*	mm	540.7 [443.6 to 739.3]	FMI	MP
Potential evapotranspiration	mm $year^{-1}$	210.1 [194.6 to 392.6]	FMI[e]	
Water balance	mm $year^{-1}$	327.8 [221 to 435.9]	FMI[e]	
Theoretical solar radiation (mean)	Mj cm^{-2} $year^{-1}$	0.5 [0.3 to 0.6]	DEM[f]	
Theoretical solar radiation (std)	Mj cm^{-2} $year^{-1}$	0.02 [<0.01 to 0.2]	DEM	
Theoretical solar radiation (range)	Mj cm^{-2} $year^{-1}$	0.2 [<0.01 to 0.7]	DEM	
TOPOGRAPHY				
Elevation (mean)	m a.s.l	308.3 [10.2 to 738.9]	DEM	

Elevation (std)	m	11.1 [0 to 127.5]	DEM	
Elevation (range)*	m	48 [0 to 414]	DEM	ER
Slope angle (mean)	^{0}	2.9 [<0.01 to 22.7]	DEM	
Slope angle (std)	^{0}	2 [0.02 to 12.9]	DEM	
Slope angle (range)	^{0}	12 [0.6 to 56.7]	DEM	
Topographical wetness index (mean)	–	10.8 [6.4 to 24.3]	DEM	
Topographical wetness index (std)	–	4.6 [0.4 to 7.7]	DEM	
Topographical wetness index (range)*	–	23.2 [9.5 to 32.8]	DEM	TWIR

a Geological Survey of Finland.

b National Land Survey of Finland.

c Generalized Additive Model (Hjort et al., unpublished data).

d Finnish Meteorological Institute. The climate variables are for the period 1981–2010.

e Methodology following Skov and Svenning (2004)

f Digital Elevation Model.

g Estimate of potential annual direct incident radiation calculated using ArcGIS 10.2 (McCune & Keon 2002)

Threatened species data

We studied threatened species from the following taxonomic groups: vascular plants, fungi, lichens, bryophytes, beetles, butterflies and moths, molluscs, mammals, two-winged flies, true bugs, birds, hymenopterans, caddisflies, stoneflies, amphibians, and spiders. The richness of each of the first eight of these (up to and including mammals) was modeled, as was that of all 16 taxa combined (the 'all' category). Threatened species were those considered critically endangered, endangered, vulnerable, or near-threatened in Finland, according to the IUCN Red List (Rassi et al. 2001). In addition, we included a few data-deficient species known to be rare (see Appendix S1 and S2 in the supporting information, for more details and the full list of species).

Geographic coordinates of the threatened species records were derived from the Hertta database (Finnish Environment Institute 2015). To ensure their spatial accuracy, we used occurrences recorded after the year 2000. 99.3% of coordinates were recorded with using GPS with 100m accuracy. There was no bias in relation to the number of species occurrences

and proximity to recreational routes (this was examined for vascular plants, bryophytes, lichens and fungi; Siikamäki et al. 2015).

As well as analysing raw threatened species richness, we modeled RWR (Williams et al., 1996; Albuquerque and Beier, 2015b). The rarity value of each species is the inverse of the number of grid cells in which it occurs. The RWR value per grid cell is the sum of the rarity values from each species recorded. Grid cells containing rarer species therefore have higher RWR. We calculated RWR for each taxonomic group with enough data (vascular plants, bryophytes, fungi) and all species combined. RWR modeling used the same environmental variables as for threatened species richness analyses, as did additional analyses of the distribution of each taxon (see Appendix S3 for the description and results of the distribution models).

Environmental variables

We compiled 24 environmental (abiotic) variables for the 6571 1km2 cells, as potential predictors (Table 1). As well as geodiversity measures (number of types of rock, soil, landform, and hydrological features), these included widely used climatic and topographic variables, to cover the most likely abiotic correlates of species diversity at the landscape scale (Field et al. 2009; Stein et al. 2014).

We derived topographic variables from a 25m-resolution digital elevation model (DEM; NLS 2000). Elevation and slope angle (mean, standard deviation and range) were calculated per grid cell using ArcMap 10.2. Topography-derived moisture conditions of the study area were calculated using the topographic wetness index (TWI; Beven & Kirkby 1979).

Detailed, expert-derived data on all the landforms in each grid cell were only available for 2083 cells, so geomorphological richness for all cells was determined by generalized additive modeling (GAM), using the available landform data and the 25m DEM, as follows (Hjort & Luoto, 2012). Landform data were derived from 1:50,000 geomorphological maps and aerial photographs (~30cm resolution). These were modeled using DEM-based and geographical variables (calibration with 1458 cells, evaluation with 625). The GAM with the final explanatory variables was recalibrated using all 2083 cells, and applied to the 8091 grid cells in this study (details in Appendix S4).

Otherwise, geodiversity per grid cell was calculated following Hjort and Luoto (2012), as follows. Hydrological richness was the sum of different hydrological feature types. Features were mapped from the National Land Survey of Finland's database (NLS 2007; Table 2) Soil-

and rock-type richness were measured by summing the number of different soil and rock types, respectively. Soil and rock types were derived from digital soil and bedrock maps, respectively, both produced by the Geological Survey of Finland (GSF 2010a, b; Table 2). Climate data for 1981–2010, at 1km^2 resolution, were derived from the Finnish Meteorological Institute (Pirinen et al. 2012; Table 1).

Table 2 The details of the features or classes, based on which geodiversity (georichness) variables are calculated.

Geodiversity variable	**Features or classes**
Rock type richness	1) ultramafic intrusive/volcanic rocks
	2) mafic intrusive/volcanic rocks
	3) intermediate intrusive/volcanic rocks
	4) granitic or fesic rocks
	5) pelitic sedimentary rocks
	6) conglomerates
	7) arkosic sedimentary rocks
	8) black schists
	9) quartz-rich sedimentary rocks
	10) sedimentary carbonate rocks or carbonatites
	11) gneisses and migmatites
	12) iron ore
	13) high-grade metamorphic rocks
	14) metasomatic rocks
	15) impact melt rocks
	16) sulphide ore
Soil type richness	1) rock (bare rock or thin soil cover; < 1m)
	2) till (glacigenic deposits)
	3) stone and block fields
	4) sand and gravel
	5) silt
	6) clay
	7) gyttja (lake and sea sediments; > 6% organic material)
	8) peat

Hydrological richness	1) lakes (size > 1ha) 2) ponds (< 1ha) 3) large rivers (> 5m wide) 4) small rivers (2–5m wide) 5) streams (<2m wide), springs

We removed highly correlated (Spearman's rank correlation coefficient, |rs| > 0.7) climatic and topographic variables after preliminary analysis, to avoid multicollinearity. Selection of the final variables was based on their mutual correlations and their conceptual relevance, and designed to obtain the same number of georichness variables as non-georichness variables (climate and topography). Therefore, two climate (representing energy and moisture availability; Hawkins et al. 2003) and two topographic variables were selected, matching the four georichness variables (Table 1). Based on the previous steps, the analyses used: rock type richness, soil type richness, geomorphological diversity, hydrological diversity, growing degree days, mean annual precipitation, elevational range, and range of the topographical wetness index.

Analysis

Boosted regression trees (BRTs) were used to analyze patterns of threatened species richness and RWR. BRTs are an ensemble modeling method that uses regression trees (from the classification and regression tree group of models) and then boosting to combine a collection of models (see Elith et al., 2008). BRT models were fitted in R version 3.1.3 (R Core Development Team 2015) using the gbm package (version 2.1.1; Ridgeway 2015) and the function gbm.step, which uses regularization methods to discourage overfitting and balance predictive performance with model fit (Hastie et al. 2001). We used a tree complexity of 4, learning rate of 0.001, bag fraction of 0.5, and a Gaussian error distribution; after experimentation, all other arguments used default values. Models were interpreted based on predictors' relative influence (RI) values, which can be thought of as model contributions. Using RI values allows these complex ensemble models to be easily interpreted. RI values are based on weighting the number of times a predictor is used for splitting a tree according to the improvement to the model as a result of each split (Friedman & Meulman 2003).

While BRTs handle datasets with many zeros reasonably well (Elith et al. 2008), very large proportions of zeros may be problematic. Further, some absences (i.e. grid cells with no threatened species records) represent locations where the conditions are too harsh for any of

the threatened species to exist, which favors climatic variables in the modeling. This is appropriate for broad-brush modeling, but geodiversity is hypothesized to be most useful in modeling biodiversity at finer scales (Lawler et al. 2015), allowing explanatory power where the environment is similar in other respects (particularly climatically). Therefore, in order to both reduce the influence of absences and constrain the analyses to climates likely to contain threatened species, we re-ran the species richness analyses with datasets in which the absence cells were sampled: we used only cells with threatened species records (presences) and cells immediately surrounding those presences. Analyses performed with the full dataset had between 6317 and 6560 absences, depending on the taxonomic group, while analyses using the sampled data had between 34 and 339 absences. This method of sampling the absences was intended to focus the resulting models more on distinguishing cells that contain threatened species from otherwise similar cells that do not (on the basis that neighboring cells tend to be similar because the environment is spatially autocorrelated), to address the hypothesis that geodiversity is important for distinguishing otherwise similar environments.

We ran BRT models both for the full set of threatened species (all 16 taxonomic groups combined), and separately for the threatened species richness of each of eight taxa with sufficient numbers of recorded threatened species to model individually. Models were run on both the sampled and the full datasets for vascular plants, fungi, beetles, bryophytes; because of data quantity, models could not be run on the sampled data for lichens, butterflies and moths, molluscs and mammals. Analyses using RWR values only involved the grid cells with threatened species records, decreasing data quantity and limiting analyses to vascular plants, bryophytes, fungi, and all species combined.

Self-statistics (SS) were used to assess internal model fit. Our models were then evaluated by using 10-fold cross-validation (CV), which, along with SS, is included in the gbm package (Ridgeway 2015). SS and CV range from 0 to 1, where a higher number suggests a better model. The cross-validation procedure randomly selects data from the area within which the model was calibrated, excludes these data from the calibration and then tests the original model on this held-back portion of data. This is repeated ten times to give an average correlation between the training and testing data. Additionally, to test whether model fit reflected more than spatial autocorrelation of the variables, we reassessed the fits of all the BRT models by geographically separating calibration and evaluation data and calculating the root mean squared error of predicted and actual values for the evaluation data. The division of the grid cells into evaluation and calibration data sets was made at the national park level by dividing the parks in an approximately east–west direction. The first dataset consisted of 46%

of the grid cells from ten national parks, which were mostly in the east, with the second dataset consisting of grid cells from the 21 remaining national parks (Fig. 1). From those two data sets, we chose the one with more presence cells in a given taxonomic group as the calibration data and the other as the evaluation data.

Results

Richness of threatened species

The best models performed well for some taxa (e.g. all species, molluscs, and vascular plants), and rather poorly for others (e.g. lepidoptera and mammals; Table 3 – models for full dataset). Not surprisingly, the more difficult task of modeling differences in the number of threatened species between similar (neighboring) cells had lower levels of success (Table 3 – 'sampled dataset').

Growing degree days and mean precipitation were usually the dominant predictors of threatened species richness, with elevational range also being important for threatened vascular plants and topographic wetness index range for bryophytes (Table 3). In terms of determining the number of threatened species present in the sampled dataset, geodiversity variables contributed relatively more than for the full dataset (Table 3); their greatest relative contribution was 24.7%, for vascular plants. Of the geodiversity variables, geomorphological richness was the most important for most taxa, while rock-type richness was the most important for lichens and vascular plants.

Using the full dataset, the combined model influence (contribution) of non-geodiversity variables varied between 86.6% (butterflies and moths) and 99.4% (molluscs), with the combined contribution of geodiversity variables therefore ranging from 0.6% to 13.4%. At this scale, the number of threatened species was thus determined primarily by climate, most of them being found in warmer and wetter areas. Geodiversity variables were modeled as being the most important in determining the number of threatened species of Lepidoptera and vascular plants (note the higher CV correlation for vascular plants, Table 3). Geodiversity variables had 1.5 to 2 times more influence in the sampled models than in the full model, and the importance of climate-relevant variables decreased.

Table 3 Cross-validation (CV) correlation and deviance, self-statistics (SS), RMSE values, and dominant (greatest relative influence/model contribution) geodiversity (GD) and non-geodiversity (Non-GD) predictors[a] and total combined geodiversity relative influence (RI; %) from Boosted Regression Tree modelling on the full (F) and sampled (S) datasets for each taxon, with the greatest contributing predictor per taxon indicated (*). RMSE = root mean square error.

	Data used (n cells)	CV corr.	CV dev.	SS mean	RMSE	Non-GD predictor with highest RI	Non-GD predictor with second highest RI	Combined non-GD model influence	GD predictor with highest RI	GD predictor with second highest RI	Combined GD model influence
ALL	**F (6571)**	0.56	1.39	0.66	1.22	MP (39.4%)*	GDD (36.9%)	**93.2%**	Rock rich (3.2%)	GM rich (2.7%)	6.8%
	S (856)	0.41	8.63	0.59	3.12	MP (41.1%)*	GDD (28.2%)	**90.3%**	Rock rich (3.7%)	GM rich (3.1%)	9.7%
Bryo-phytes	**F (6571)**	0.40	0.05	0.57	0.14	GDD (32.1%)*	MP (26.1%)	**90.2%**	GM rich (5.6%)	Rock rich (2.8%)	9.8%
	S (191)	0.06	1.20	0.46	0.80	TWIR (27.3%)*	GDD (24.4%)	**78.8%**	GM rich (9.5%)	Hydro rich (8.4%)	21.2%
Beetles	**F (6571)**	0.34	0.04	0.51	0.15	GDD (63.2%)*	MP (20.3%)	**92.9%**	GM rich (5.2%)	Rock rich (0.8%)	7.1%
	S (110)	0.14	1.64	0.50	0.96	GDD (35.4%)*	ER (25.5%)	**87.7%**	GM rich (7.7%)	Rock rich (2.3%)	12.3%
Fungi	**F (6571)**	0.38	0.60	0.53	0.71	MP (41.1%)*	GDD (36.4%)	**94.5%**	GM rich (3.2%)	Soil rich (1.1%)	5.5%
	S (593)	0.22	5.11	0.48	1.89	MP (36.3%)*	GDD (25.5%)	**85.6%**	GM rich (8.2%)	Hydro rich (3.6%)	14.4%
Lepid-optera	**F (6571)**	0.28	0.01	0.42	0.05	MP (62.48%)*	GDD (16.4%)	**86.6%**	GM rich (9.6%)	Soil rich (2.3%)	13.4%
Lichens	**F (6571)**	0.33	0.23	0.54	0.50	GDD (53.7%)*	MP (38.9%)	**95.7%**	Rock rich (2.7%)	GM rich (1.3%)	4.3%
Mam-mals	**F (6571)**	0.22	<0.01	0.47	0.05	GDD (38.0%)*	MP (35.6%)	**93.6%**	GM rich (3.1%)	Soil rich (2.7%)	6.4%
Moll-uscs	**F (6571)**	0.58	<0.01	0.59	0.04	GDD (69.5%)*	MP (25.3%)	**99.4%**	GM rich (0.5%)	Rock rich (0.1%)	0.6%
Vas-cular plants	**F (6571)**	0.59	0.09	0.72	0.17	GDD (29.3%)*	ER (24.3%)	**88.3%**	Rock rich (4.8%)	GM rich (3.5%)	11.7%
	S (319)	0.44	1.08	0.66	0.79	ER (30.0%)*	GDD (19.1%)	**75.3%**	Hydro rich (11.6%)	GM rich (9.1%)	24.7%

[a] All predictors in the table showed a positive correlation between the variable and predicted species richness in the models. See Table 1 for the explanation of variable abbreviations.

Table 4 Analysis of rarity-weighted richness (RWR), in relation to the geodiversity, and climate and topography predictors, including self-statistics (SS) and cross-validation statistics (CV): **(–)** indicates negative relationship between predictor and RWR; CNGD=combined non-geodiversity predictors' absolute model influence; CGD=combined geodiversity predictors' absolute model influence; predictor abbreviations are listed in Table 1.

			Abiotic predictor relative influence (%)									
	SS	**CV**	**GDD**	**MP**	**ER**	**TWIR**	**CNGD**	**Rock rich**	**Soil rich**	**GM rich**	**Hydro rich**	**CGD**
ALL	0.58	0.33	27.07	-26.08	27.54	7.93(–)	**88.62**	6.58	0.55(–)	3.16(–)	1.09	**11.38**
Bryophytes	0.55	0.41	49.21(–)	-5.55	6.02	6.95	**67.73**	0.04 (–)	30.02	1.84	0.37(–)	**32.27**
Fungi	0.59	0.28	44.33	18.57	7.58	22.78	**93.26**	0.07	0.10	0.49	6.08	**6.74**
Vascular plants	0.62	0.19	27.39	10.92(–)	13.98(–)	7.09	**59.38**	8.13	12.85	6.38	13.26	**40.62**

Rarity-weighted richness of threatened species

RWR of threatened species was analyzed for vascular plants, bryophytes, fungi, and all species combined. Growing degree days was strongly positively related to RWR for vascular plants, fungi, and all species combined, while this relationship was negative for bryophytes (Table 4). Greater RWR of threatened species was also associated with: higher rainfall, topographic wetness index range, and hydrological richness for fungi; lower rainfall and elevational range, and higher hydrological richness and soil type richness for vascular plants; higher soil type richness for bryophytes; and lower rainfall and higher elevational range and rock richness for total threatened species richness. Internal model fits (self-statistics) were reasonable, but cross-validation statistics were weaker. Compared with the threatened species richness models, the combined effect of geodiversity variables was clearly greater for vascular plants and bryophytes in the RWR analyses; for fungi and for all species combined, there was little such difference.

Discussion

Our results from modeling the diversity of 271 threatened species across Finnish national parks revealed that the number of growing degree days and mean annual precipitation were of the greatest importance for threatened species richness (both raw and weighted by rarity). Elevational range, a widely used topographic metric, was also important. These results are reassuring given the large body of knowledge built up over centuries with regard to overall species richness (Field et al. 2009; Stein et al. 2014). The use of geodiversity – the richness of rock types, soil types, geomorphological features, and hydrology – improved the model predictions, especially when we sampled the data to include only the range of environments in which threatened species are known to occur. This suggests that climatic gradients may determine the regional species pools, while geophysical factors and local heterogeneity have a greater influence at finer scales. To assess the effect of the sampling strategy, we also ran BRT models using a random subset of absence cells; the results were very similar to those reported herein. Furthermore, our results are to some extent contingent on the identities and relative numbers of variables used in the analysis, though our exploratory data analysis and model checking indicated that our conclusions are robust to these issues.

Our findings are consistent with our first study hypothesis (H1), and with previous studies that indicate that thermal conditions and energy availability are among the major limiting factors of species patterns in high latitudes, especially at large geographic extents (Hawkins et al. 2003; Field et al. 2009). This should apply particularly to Finland, which is a long and quite narrow country running over 1000 km north to south, thus having a strong latitudinal gradient in climate. Sampling the data controlled climate to some extent because it removed from consideration the cells that are far from places with threatened species. Even so, the cells span nearly the whole of Finland, and climate remained fairly dominant in the models.

Although the strong modeled effect of growing degree days was consistent and always positive, threatened species richness of different taxonomic groups demonstrated unique relationships with climate, topography and geodiversity variables, in line with the habitat heterogeneity hypothesis (H2). This was most prominent in analyses of the sampled data, where absences were restricted to cells neighboring presences. We found support specifically for the hypothesis that geodiversity variables improve models over and above climate and topography (H3). In the models, geodiversity variables generally showed relatively small (in line with Anderson et al. 2015) but consistent additive effects, and improved the diversity

models' predictive ability for beetles, bryophytes, and vascular plants. Geodiversity predictors were most important when using the sampled data, rather than the full dataset. Thus, while climate is a key driving force, explicitly conserving the diversity of geophysical settings may offer an approach to conservation that manages to protect both abiotic and biotic diversity in a dynamic climate.

Of the geodiversity variables, rock type richness was relatively important for the richness (raw and rarity-weighted) of threatened vascular plant species and for threatened lichen species richness. Elsewhere, rock richness has been firmly linked to biodiversity of lichens (Spitale & Nascimbene 2012) and plants (e.g. Pausas et al. 2003; Kougioumoutzis & Tiniakou 2014). Geomorphological richness was consistently significant (if not always strong) in our models, especially for raw threatened species richness. Geomorphological features are known to provide unique abiotic conditions (Nichols et al. 1998; Hjort et al. 2015), and may promote threatened species diversity (Bétard 2013).

Soil and hydrology both contributed significantly to our models of richness and RWR. Soil type diversity was important for the RWR of threatened bryophytes and vascular plants, consistent with claims that soil type diversity affects vegetation (e.g. Stein et al. 2014). Although aquatic environments are not the main habitat for many threatened vascular plants in boreal environment, several species occupy habitats near water, such as streams and ponds (e.g. *Saxifraga hirculus*; Rassi et al. 2010), which might explain the importance of hydrological richness in models for threatened vascular plant species richness (raw and rarity-weighted).

We postulated (H4) that threatened species can be modeled successfully using climate, topography, and geodiversity variables. Models based on the full dataset performed well, whereas models using the sampled data showed more varying performance. These results are consistent with climate being the main control of species patterns at large extents (Hawkins et al. 2003; Field et al. 2009); climate can be used to provide the first cut for predicting threatened species diversity and distribution at a regional or national scale. By constraining absences to being within 1km of the presence of a threatened species, sampling the data removed the most climatically unsuitable grid cells, thus reducing the ranges of the climatic variables and making reduction in the explanatory power of climate almost inevitable. This left a dataset comprising cells that are climatically suitable for at least some threatened species – and one for which the absences are therefore harder to predict. It is for such cells that geodiversity variables should be, and were, most useful. Indeed, these variables may represent the next set of abiotic requirements once the climatic tolerance filter has been passed through.

In the analyses of RWR of threatened vascular plant and fungal species, the combined contribution from geodiversity variables exceeded the equivalent contribution in the raw threatened species richness models (Tables 2, 3). Thus geodiversity appears to be particularly useful for understanding patterns of threatened species diversity when site complementarity is considered. Even so, as with the raw richness of threatened species analyses, climate variables dominated our analyses. Interestingly, growing degree days was strongly negatively associated with RWR for bryophytes. The most infrequently occurring bryophytes in Finland therefore appear to be found in relatively cold areas with short growing seasons and also greater mineral and nutrient diversity from a greater variety of soils (Rassi et al. 2010). In a practical sense, we see value in conducting analyses such as ours, for threatened species data, to most effectively allocate conservation resources; geodiversity data can be used alongside other climate and topography data to better target areas that support rare and irreplaceable communities (Albuquerque & Beier 2015c).

Both abiotic environmental heterogeneity (Stein et al. 2014) and geodiversity (Gray 2013) have been described and measured in a wide variety of ways. It is likely that the best measure to use will be specific to the study area and taxon, but methodologies should be transparent, and transferable where possible. In this study, we used simple measures of geodiversity, providing a time-saving and financially practical way of measuring abiotic environmental heterogeneity of the uniformly sized study units. These geodiversity measures complement broad-brush topographic variables (e.g. elevational range) that are commonly used in analyses of biodiversity, and represent a more detailed appraisal of the abiotic environment. Often, geodiversity is defined to include topographic data (e.g. Parks & Mulligan 2010), and doing so would considerably increase the influence of 'geodiversity' in our analyses. However, we see value in distinguishing between these different aspects of environmental heterogeneity, and analysing the effects of explicit measures of geology, landforms, and hydrology.

In future studies, consideration of specific geosites, including geological objects or fragments of the geological environment exposed on the land surface, and not just overall geodiversity, could improve our models and our understanding of biodiversity (Hjort et al. 2015). It would also be useful to study the relationship between biodiversity and different measures of geodiversity (measures other than richness), because these relationships are likely to depend on the metrics used. The positive relationship between overall species richness and geodiversity is becoming reasonably well established in literature, but the connection between threatened species and geodiversity deserves more attention in future

research; we hope we have made a useful start herein. In conclusion, we stress the need for wider incorporation of geodiversity – not just DEM-based topographic variables – into ecology and macroecology, and into both conservation theory and management.

Supporting Information

Information on the taxonomic groups included in the study (Appendix S1), the species list (Appendix S2), the species distribution modelling analyses (Appendix S3), and details of the modelling procedure of geomorphological richness (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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PAPER IV: MODELLING COMMON AND RARE PLANT DIVERSITY AND DISTRIBUTIONS IN RELATION TO GEODIVERSITY IN AN UPLAND LANDSCAPE

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Abstract

Context Recent research suggests that novel geodiversity data on landforms, hydrology and land-surface materials improve models of the spatial distributions and diversity of species at the landscape scale by quantifying abiotic variability more effectively than widely-used measures of spatial heterogeneity. However, our understanding of the role of geodiversity in modelling species' distributions is generally lacking, especially for rare species.

Objectives We aimed to relate macro-scale controls of biodiversity and species' distributions with explicit geophysical and climatic landscape characteristics for common and rare plant species separately at a scale that is highly relevant to conservation.

Methods We automatically extracted landform information using geomorphometry and compiled hydrological and surface material data from existing sources. We used these data alongside topography and climate-relevant predictors to model the distributions and total numbers of rare (N=469) and common (N=1,434) plant species, separately, at 1km^2 resolution for the Cairngorms National Park, Scotland.

Results Previously recognised fine-scale relationships are detectable at macroecological and landscape scales, according to our findings, and geodiversity significantly improved our models, in which climate and topography contributed the most to the models. The inclusion of novel geodiversity data, and its constituent geofeatures, revealed previously unknown links between species and the geophysical environment at this macroecological scale. For example, species' distributions were linked to soil mineralogy (e.g. the rare *Alchemilla wichurae*) and the coverage of specific landforms (e.g. mountain hollows).

Conclusions We believe that the conceptual and empirical gains from geodiversity make its incorporation alongside widely-used topography and climate-relevant variables not only worthwhile, but advisable. These data may more successfully capture facets of the abiotic environment that are closely linked to ecological processes, making such findings important in the context of both theory and management. Novel geodiversity data extracted using geomorphometry were of particular value.

Introduction

Environmental change and biodiversity loss are threatening ecosystem functionality in many habitats globally (Oliver et al., 2015). Common species (those with relatively high abundances) are thought to drive much of the functioning of an ecosystem, and the associated services

(Winfree et al., 2015). However, rare species have been identified as being able to make significant ecosystem, and ecosystem service, contributions (Lyons et al., 2005; Gascon et al., 2015), as well as encompassing a bequest value (Richardson and Loomis, 2009). Rare species may also be at greater risk from environmental change (Moritz and Agudo, 2013), thus increasing the need their conservation prioritisation. Meanwhile, the importance of total species diversity for ecosystem health, function, and services is widely reported (Isbell et al., 2011; Hautier et al., 2015). Advancing our knowledge of landscape-scale correlates of species' distributions and biodiversity is therefore of theoretical and practical relevance.

Macroecological work has tended to be conducted at broader scales than that of the landscape, and either focus mainly on species richness, which itself tells us mainly about common species (Gaston, 2010), or on species distribution modelling (SDM) using climatic envelopes. Such SDMs suffer from the unrealistic assumption that species' realized niches are the same as their fundamental niches and assessments of rare species using this method typically suffer badly from small sample sizes and fail to include abiotic data that relate closely to ecological processes (Kearney & Porter, 2009; Zimmermann et al., 2010). Meanwhile, ecological studies using small plots across a limited extent can be too autecological and fail to consider landscape-scale drivers of observed biodiversity and species' distributions (Boyd et al., 2013). To bridge this gap, we need predictors that are capable of capturing ecologically relevant geophysical characteristics of the landscape.

This gap has often been approached using measures of spatial environmental heterogeneity, which describes the diversity of the physical environment, and its relationship with biodiversity and species' distributions is firmly documented, especially at the landscape scale where climate tends to be more constant than it is for larger study areas (Stein et al, 2014). Heterogeneity quantification methods are varied, but most commonly they include widely-used topographic measures such as mean and range of elevation and slope. Although their value in macroecology has been shown repeatedly across taxa and scales (e.g. Pausas et al., 2003; Dufour et al., 2006; Lundholm, 2009; Parks and Mulligan, 2010; Stein et al., 2014), these relatively crude topographic measures may oversimplify the physical environment, thus precluding a more advanced ecological understanding (Hjort et al., 2012; Lawler et al., 2015). We argue that existing explicit landform quantification techniques (i.e. automatic landform extraction – geomorphometry), which are largely confined to the field of geomorphology may be able to inform our ecological knowledge and advance the way that we measure heterogeneity at the landscape scale.

Data on landforms, hydrology, and geology may be considered under the term 'geodiversity', which we define as "the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms" (after Bailey et al., 2017: also see Hjort et al., 2012; Gray, 2013). Here, we expressly make an important conceptual distinction between geodiversity and widely-used measures of topography (these may refer to range in elevation and slope or topographic openness, for example). Geodiversity comprises 'geofeatures' whereby an individual landform (e.g. a hollow in a mountainside) or area of a given surface material (e.g. an area calcium carbonate rich bedrock) is a 'geofeature' (Table 1). In turn, the quantified geofeature is referred to as a 'geodiversity component', or 'GDC' (Bailey et al., 2017). GDCs could therefore be, for example: the areal coverage of a landform or geological type, the length of a stream, or the number of soil types in a given area.

Geodiversity, also called 'geophysical diversity', has previously been demonstrated as a useful predictor of biodiversity at landscape scales (Barthlott et al., 2007; Hjort et al., 2012; Lawler et al., 2015; Tukiainen et al., 2017). The relevance of the landscape scale was demonstrated in a cross-scale study, which found that geodiversity is more important at the landscape scale than at larger geographic extents for native and, less so, alien vascular plant species richness (Bailey et al. 2017). Geodiversity advances heterogeneity research by allowing us to capture dimensions of the physical environment that are missed or oversimplified by relatively crude topographic metrics. However, most studies to date (e.g. Hjort et al., 2012; Kougioumoutzis & Tiniakou, 2015) have used a compound geodiversity metric, which may overlook important contributions from individual geofeatures. There is still much to be done, however, and increasing our knowledge of the role of geofeatures, including soil systems and landforms, is important for understanding and managing changes in biodiversity and individual species' distributions (Brazier et al., 2012). Geofeatures may have much relevance to species' distributions and biodiversity through their implicit links to abiotic processes (e.g. disturbance, weathering, small-scale hydrology) and properties (e.g. nutrient levels, microclimate) and associated ecological theories surrounding the niche, biotic heterogeneity (habitat variety) and local resource availability (Dufour et al., 2006; Viles et al., 2008; Hjort et al., 2012; Bétard, 2013; le Roux et al., 2013; Hjort et al., 2015). Meanwhile, geodiverse locations might be important for species' persistence under climate change (Albano, 2015).

Incorporating landform geofeatures into modelling requires ways of quantifying them because geomorphological maps across wide areas are rare, and simply do not exist for many places. Geomorphometry, the automated extraction of land surface information from digital elevation models using relational geometry, offers a solution to this problem and provides ecologically-meaningful data. However, such techniques have seldom been employed in

ecology and macroecology (except see Theobald et al., 2015; Bailey et al., 2017), being confined to the fields of geomorphology and geosciences, for example. We use geomorphometry-derived landform data in our biodiversity and species' distribution models alongside other existing land surface material and hydrology data for an upland landscape in Great Britain: Cairngorms National Park in the Central Scottish Highlands. This area is consistently mapped for its geology in much the same way as the rest of Great Britain but not for geomorphological landforms, thus necessitating geomorphometry. It therefore provides a highly suitable place in which to examine these techniques at the landscape scale. Furthermore, a recently-compiled rare species database is available, allowing us to explore the taxonomic limits of the geodiversity concept, whilst moving towards an improved understand of rare species' relationship with the geophysical environment.at the landscape scale.

The sensitivity of upland British landscapes, including the Cairngorms, has been previously highlighted (e.g. Gordon et al., 2001; Thomas, 2012), as well as the need to ensure that the abiotic environment has space to adapt as geomorphological and soil processes change with climate (Brazier et al., 2012). However, landscape-scale analyses relating ecology to the geophysical environment are lacking; geodiversity provides an avenue by which to study this. Relating species' distributions and richness (the biodiversity metric used here) to the current geophysical environment should be informative in the context of where to focus management efforts and in relation to known landscape sensitivities, as well as for advancing our scientific understanding. Specifically, we aimed to: (i) relate macro-scale controls of biodiversity and species' distributions (e.g. climate) with explicit landscape characteristics (e.g. landforms); (ii) analyse common and rare (rare species defined broadly) species separately to determine the key contributions that geodiversity data can make over and above climate and standard topographic variables at a scale that is highly relevant to conservation; and (iii) use a novel geomorphometric technique to derive landform data, which have typically been hard to obtain, and thus assess the potential value of such automated techniques for generating new landscape-relevant data.

Methods

Study area

The Cairngorms National Park ('the Cairngorms'; Fig. 1a), located in the Scottish Highlands, is the largest and highest national park in Great Britain. About half of its area is considered as internationally important under European law (Amphlett, 2013). The sensitivity of this

landscape as well as the value of its geoheritage is widely reported (Gordon and Sutherland, 1998; Gordon et al., 2001). Collectively, the mountains form a number of granite plateaus with deep passes in between, making for a topographically complex environment. Indeed, there is a substantial range in elevation (mean elevation of 533 m; min = 97; max = 1309) and slope (mean = 11°; min = 0°; max = 72°) across the area (statistics derived from a 10 m DEM).

Windy, cool and humid conditions dominate. Higher-elevation areas experience weather and climate similar to that of the alpine semi-tundra. Mean precipitation ranges from 800 mm to 1500 mm per year and is broadly linked to altitude. However, the eastern areas are drier because of the predominant westerly direction of approach of Scotland's weather, meaning that much precipitation falls when weather systems encounter the western mountains. Pre-glacial landforms are extensive and include palaeosurfaces and breaks of slope, topographic basins, valleys, domes and tors (Hall et al., 2013). Glacial landforms are marked by sudden breaks from the gentler pre-glacial mountain forms and include corries and roches moutonnées (Sugden, 1968; Gordon and Sutherland, 1993), alongside periglacial features such as rock glaciers and boulder fields. At higher elevations, alpine, low alpine, and sub-alpine habitats are present. More widely, heather moorland and native pinewoods dominate the area, with deciduous trees in many places. Snow-bed communities, which include rare and specialised liverworts and mosses, can also be found. Blanket bog habitats are present, especially on the high plateaus. More details on the study area are provided in Appendix S2.

Data

All predictor sets and subsets are summarised in Table 1. Except for geomorphometric analyses (below), all data for the Cairngorms National Park study area were processed and joined to 1 km2 British National Grid (BNG) cells (n = 4,774) using ArcGIS 10.2, and subsequently processed and analysed in R (R Core Team, 2017). Grid cells with < 75% land area within the Cairngorms were removed. Every $1km^2$ grid cell in the study area contains vegetation in reality, so grid cells with no data were removed from the analysis because they must not have been sampled in the study period (or at all).

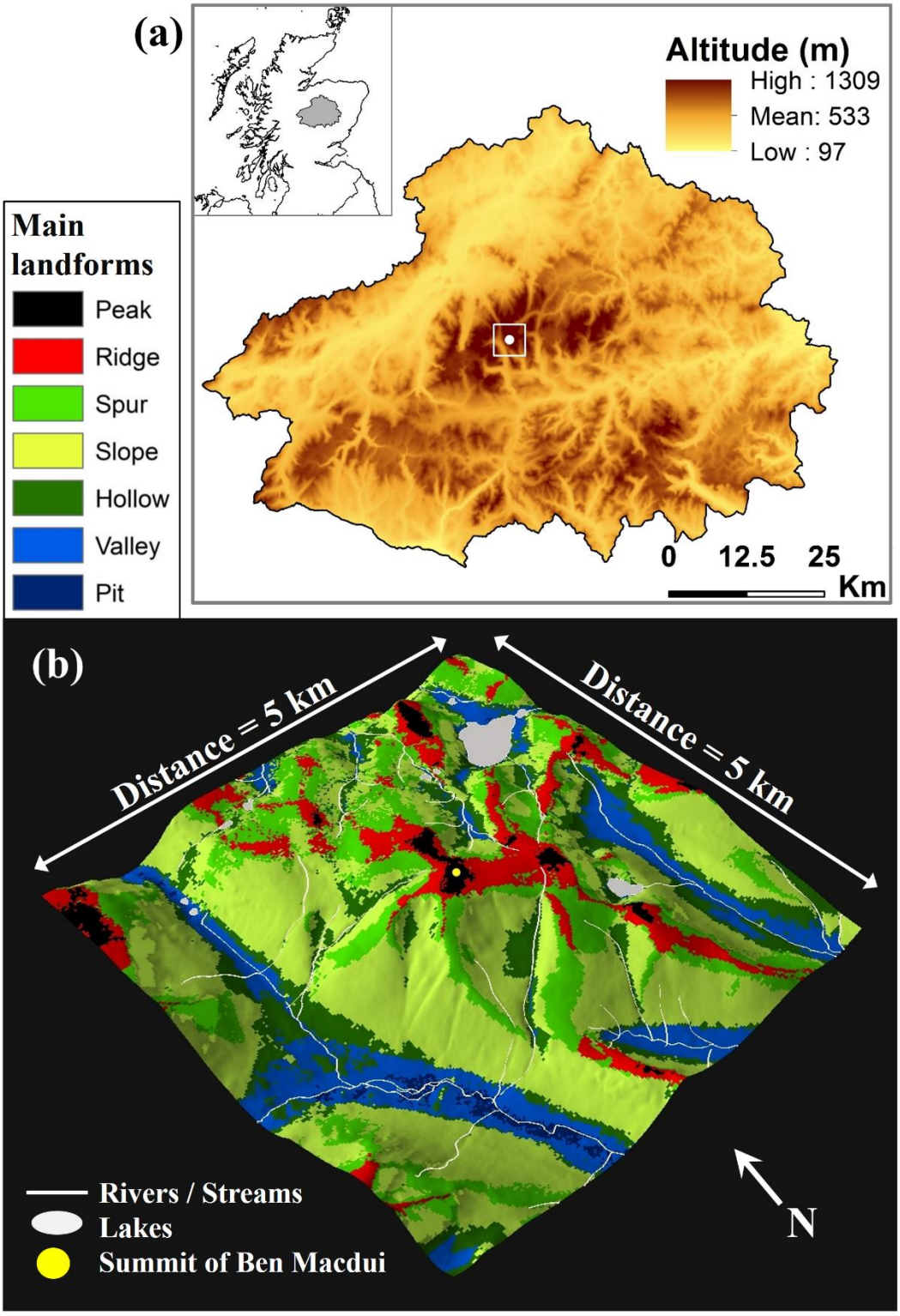


Figure 1 (a) elevation map of the Cairngorms National Park (CNP) with an inset showing CNP shaded gray within Scotland. (b) A 3D visualisation of the geomorphometric landform classification (produced using r.geomorphon in GRASS GIS 7.1) designed in ArcScene 10.2. (b) is centred over Ben Macdui (height = 1,309 m – the highest point in the Cairngorms), which is shown with the yellow circle in the centre of the image. Rivers and lakes are shown as white lines and polygons, respectively. The map in (a) uses a 10m elevation raster, derived from Intermap Technologies NEXTMap (accessed via NERC Earth Observation Data Centre; Table 1).

Table 1 Details of the variables within each predictor set. [1]Jasiewicz and Stepinski (2013); [2]Intermap (www.intermap.com); [3]NEODC = National Environment Research Council (United Kingdom) Earth Observation Data Centre (neodc.nerc.ac.uk); 'OS' = Ordnance Survey.

Predictor set	[Category] Variable (notes)	Resolution/ scale	Value per 1x1 km grid cell	Source
Geodiversity components (GDCs)	[Landforms] Areal landform: coverage of ridges, slopes, spurs, peaks, pits, hollows, valleys, and flat areas.	10 m	Areal coverage r.geomorphon[1]	Derived from NEXTMap data (Intermap via NEODC)[2,3] in GRASS GIS 7.1.
	[Materials] Soil parent material mineralogy and texture	1:50,000	Number and coverage of superficial deposit types	British Geological Survey (BGS) under Academic License
	[Hydrology] River length	1:50,000	Total length	OS Strategi via Edina Digimap
	[Hydrology] Lake area	1:50,000	Areal coverage	OS Strategi via Edina Digimap
Climate-relevant predictors	Longitude (precipitation proxy)	1x1 km	Longitude	British National Grid via OS Strategi via Edina Digimap
	Elevation (temperature proxy)	10 m	Mean	NEXTMap data (Intermap via NEODC)[2,3]
Topography	Elevation and slope (land surface parameters)	10 m	Mean and standard deviation	NEXTMap data (Intermap via NEODC)[2,3]

Widely-used topographic variables were calculated for each grid cell from the NEXTMap 5 x 5 m digital elevation model, which we resampled to 10 x 10 m to reduce noise (Table 1). These were the mean and standard deviation in elevation and slope. Direct measurements of climatic conditions were not available at a sufficient resolution for this area. However, elevation can be considered as a climate-relevant predictor as it is strongly related to temperature. The longitude of the centroid of each grid cell was also included because there is longitudinal variation in climate, particularly precipitation, in this area (outlined below).

We compiled geodiversity data (landforms, hydrology, and geology) from existing datasets and automated extraction of landform coverage information using geomorphometry. We obtained data on rivers and lakes under open license from the Ordnance Survey's 'OpenData' service (Appendix S1 in Supporting Information). We checked these data against 1:50,000 OS base maps and additions made (by digitisation in ArcMap) for smaller streams where appropriate. Using the 1:50,000 British Geological Survey (BGS) Soil-Parent Material

Database, under academic license, we calculated the dominant mineral coverage of the soil's parent material (PM) and its diversity (count of different types) per grid cell. There were 18 classes in total, including, but not limited to: acid, basic, calcium carbonate, clay-silica, organic, mixed. Soil parent materials define geological deposits over which and within which soil develops and are closely related to the soil's mineralogy, drainage, and texture. Soil texture data were also extracted. Parent material mineralogy and texture are important for soil formation because of how they affect weathering processes and for vegetation because of the acidy, alkalinity, and coarseness.

We produced landform coverage data using geomorphometry, specifically the `r.geomorphon` algorithm developed by Jasiewicz & Stepinski (2013), in GRASS GIS 7.1 (GRASS Development Team, 2017). The following landforms and features were mapped in raster format and their areal coverage calculated for each grid cell: peaks, ridges, shoulders, spurs, slopes, footslopes, hollows, valleys, flat areas and pits (Fig. 1b). Raster grid cells in the geomorphometry data were removed if they overlapped with known lakes. This was particularly common for 'pits', as would be expected. Some pits were near river channels but visual observation indicates that they are often located away from river channels, as well. Indeed, pits may represent depressions in the landscape that are hydrologically (or otherwise) significant (perhaps bogs or ponds, for example), but are not mapped as hydrological features.

Species' occurrence data were provided by the Botanical Society of Britain and Ireland (BSBI) via the Distribution Database at a resolution of 1 km^2 using the British National Grid. The BSBI hosts a single database (the 'Distribution Database') to which data are contributed by its volunteers and coordinators – who are strongly encouraged to use unbiased sampling (Walker et al., 2010). We used accepted data records (those verified within the database) collected between January 1995 and April 2016. The Cairngorms 'Rare Plant Register' (RPR) was used to identify rare species records for the area (Amphlett, 2013), while other species records are classified as 'common' in this study. The definition of 'rare' species is a broad one and comprises species that are listed on the UK Red List; UK Biodiversity Action Plan; Scottish Biodiversity List; and Wildlife and Countryside Act; or species which are considered to be: endemic, native, or archaeophyte (if rare in the Cairngorms or of cultural significance) within the Cairngorms; nationally rare or scarce; a European Protected species (Amphlett, 2013). In the interest of data quantity, this broad definition of 'rare' was maintained.

There was no overlap between our 'rare' and 'common' species lists. There were 469 rare species in total (maximum richness of 39), and at least one rare species was present in 1,640 grid cells (34.6% of the total number of grid cells in CNP), while there were 1,434

common species (maximum richness of 294), which were present in 1,757 grid cells (36.8%). The fact that many cells contain only rare species can be explained by the broad definition of rare species used by this dataset, within which some species will be locally common. Additionally, the BSBI may carry out specific rare species surveys in some areas. Despite the BSBI's sampling approach, the distribution of species records is somewhat clustered, with largely unsurveyed areas interspersed with well surveyed areas, the latter of which, naturally, are often in more accessible parts of this largely remote landscape (Fig. 2).

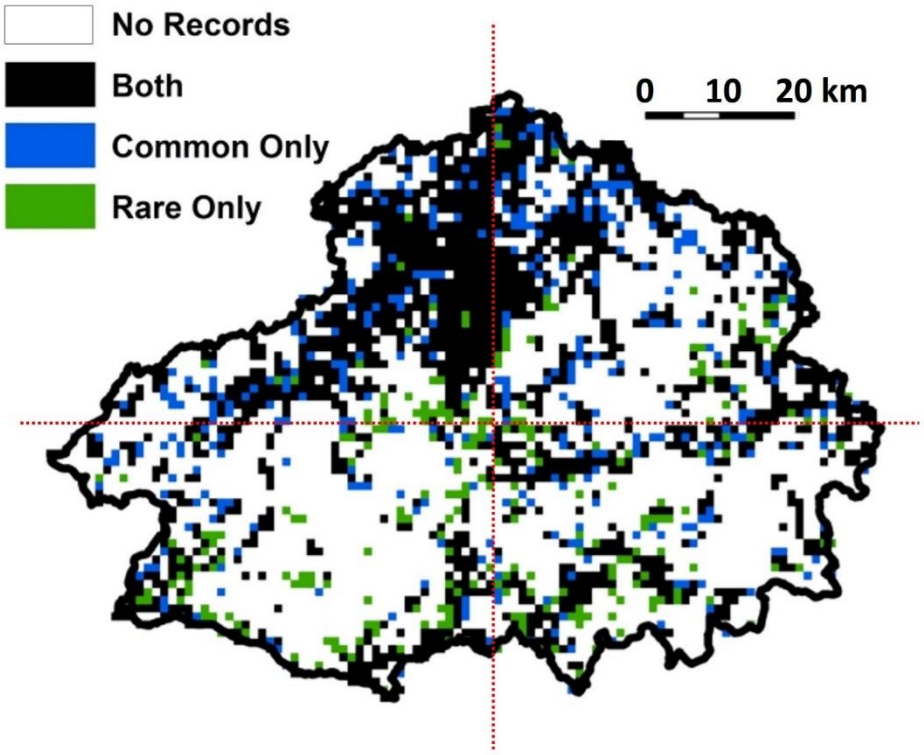


Figure 2 The distribution of rare and common species occurrences on the 1x1 km grid used (blue = common records only; green = rare only; black = both) within the Cairngorms National Park. The geographic split of the study area into (north, east, south, west) is also shown.

Analysis

Statistical models were developed for common and rare species diversity (using species richness values per grid cell) and species' distributions (using binary presence–absence data as the response). This therefore produced one model for rare species richness, one for common, and then one model for each species distribution. Models were produced for the whole of the study area, and for the north, east, south, and west individually to determine whether patterns were comparable in different areas of this landscape (geographic split shown in Fig. 2). Results are always presented for the whole area, unless they differed substantially, in which case this is noted.

To model both species richness and individual species distributions, we used boosted regression trees (BRTs, a machine learning technique) in R 3.2.0 (R Core Team, 2017). With such a complex dataset and largely unknown relationships (especially regarding geodiversity) over many different geographical contexts with variable collinearities and interactions, using a machine learning algorithm was preferable. Additionally, BRTs explicitly consider interactions between variables, which can point towards important combined effects, as well as dealing with non-linearity and collinearity reasonably well relative to other methods (Dormann et al., 2013). This technique is also appropriate for binary and continuous response variables (i.e. presence–absence and species richness, respectively). More of this technique's advantages can be found in Elith et al. (2008).

We used `gbm.step` (gbm 2.1.1 package in R; Ridgeway, 2015) to implement the BRTs. This function uses shrinkage procedures as each tree is added, helping to control the number of terms to produce a more parsimonious model, and tries to avoid overfitting by using regularisation methods. To study individual predictors' model effects, the contribution (relative model influence) of each predictor on the model outcome was obtained. These are scaled to add up to 100, where a value of 100 for a predictor would mean that only that predictor contributed to the final model. Furthermore, the correlation between a predictor and the response variable (i.e. species richness or a species' distribution) was calculated and the direction of the relationship applied to the model contribution value to make it appear negative where it had a negative relationship with the response. This makes the results more readily interpretable.

We used three predictor sets, which were: (i) geodiversity; (ii) climate (for which the proxies were longitude and elevation); and (iii) standard topography (mean slope and standard deviation in elevation and slope) (Table 1). Within geodiversity, the following subsets were used: landforms, surface materials, and hydrology

(i) climate and standard topography [elevation standard deviation and slope mean and standard deviation]; (ii) landforms [all landform coverage data from geomorphometry]; (iii) hydrology; (iv) soil parent material (PM) coverage and richness. Furthermore, two parameters were used for soil PM and separate models were run for each. These were: (i) dominant mineral coverage/variety (e.g. soil PM dominated by silica) and (ii) texture group coverage/variety (e.g. light or heavy, sandy or silty, etc). All soil PM parameters in the dataset were inferred from the bedrock and there are inevitably collinearities between texture and dominant mineral coverage, which is why these variables were not all included in the same models.

Most default parameters within `gbm.step` were maintained, with a tree complexity of 3 allowing (up to) three-way interactions (Elith et al., 2008), a bag fraction of 0.5, and a preferred learning rate of 0.05, which was occasionally reduced to 0.01, 0.005, and then 0.001 according to data requirements. Predictors contributing <10% (or sometimes <7.5% where the former removed too many variables) were removed from the initial model, which was rerun with the simplified predictor set to produce the final results.

As well as evaluation from internal fit statistics (self-statistics), models were validated using 10-fold cross-validation in the `gbm` package. This approach randomly subsamples the data ten times according to the user-defined bag fraction (here 0.5, or 50%) and tests the model produced on this held back portion of data. The mean correlation between the training and each testing dataset is then reported. We multiplied SS and CV values, which were originally numbered between 0 and 1, by 100: a value of 100 would be a model that explains all of the variation in the data (SS) or predicts well to new data in the same area (CV), while 0 indicates a very poor model. Models were run with and without GDCs and model statistics compared.

Results

The coverage of soil parent material (PM) type, measured according to the dominant mineral, contributed highly to the models, and especially so for rare species' distributions (Fig. 3). Landform coverage was consistently positively related to species' presences and overall richness: this contribution was similar for common and rare species, with a marginally higher median for common species' distributions and rare species diversity. The contribution was also higher than that of standard topography variables, but lower than the combined climatic variables' model contribution. Hydrology and the variability in soil parent material was less

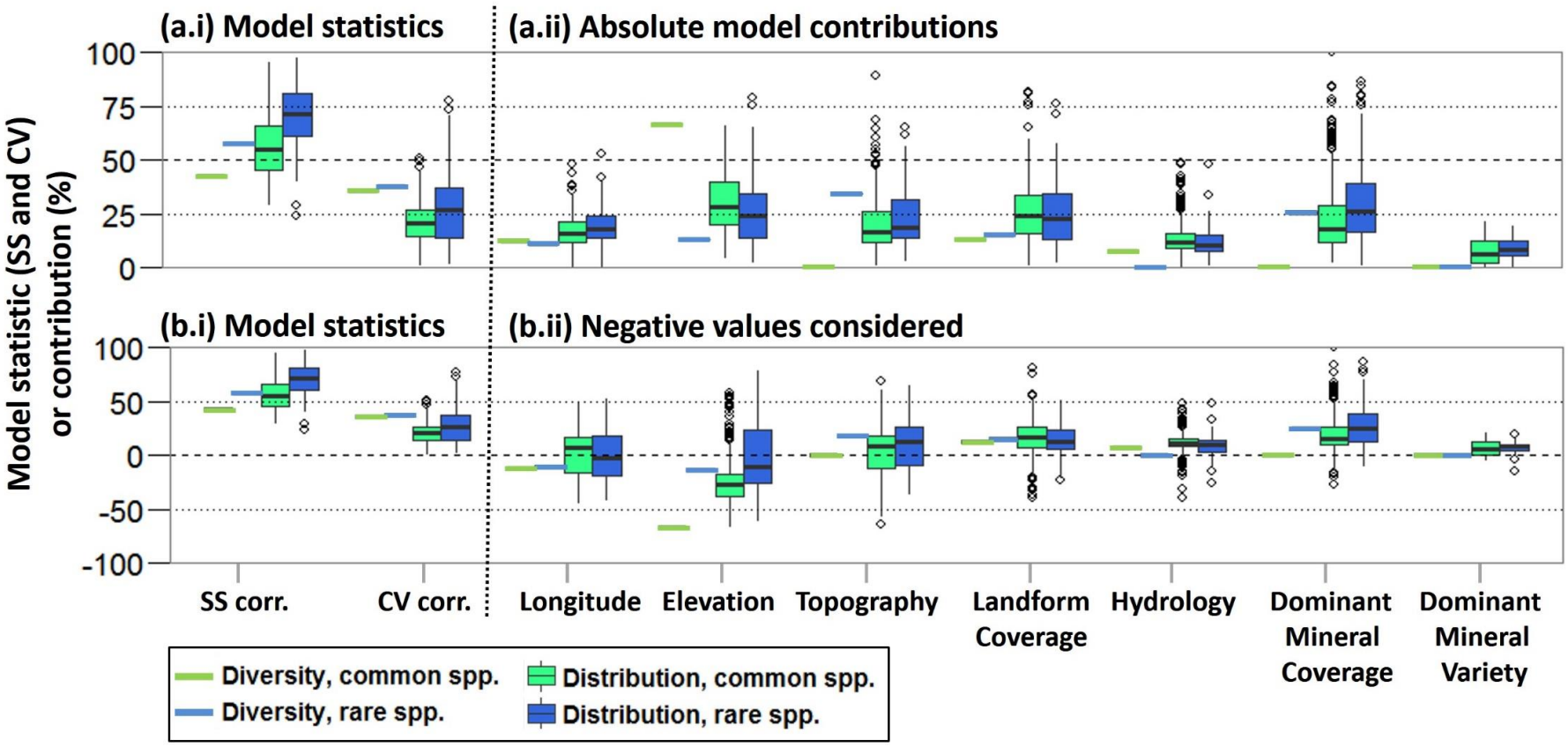


Figure 3 Model statistics (a.i and b.i) and model contributions from model predictors (a.ii and b.ii) for models of species diversity (one model for common and one for rare species) and species' distributions (results across models for each individual species) for all common (green, always on left) and rare (blue, always on right) species across the whole of the Cairngorms National Park. These are broadly reflective of patterns seen in the north, east, south, and west individually. Model fit (SS) and evaluation (CV) statistics have been multiple by 100 for purposes of plotting. (a.ii) uses the absolute model contribution (0 – 100%), while (b.ii) corrects for negative correlations (-100 to 100). Model contributions have been combined for each predictor set (see Table 1). Appendix S4 shows these results for each individual area in this figure and Appendix S5 is as S4 but shows the results when soil parent material texture was used instead of mineralogy.

important and was also similar for rare and common species' distributions and common species diversity. The variability in soil PM texture and dominant mineral contributed only a little. Model interactions were highly idiosyncratic between the species. Generally, however, an interaction between longitude and elevation, which were not collinear across the whole Cairngorms area, frequently accounted for the dominant interaction in the models. The same can also be said of slope standard deviation and mean elevation, and mean elevation and river length.

Elevation was the highest contributing predictor to rare (13%) and, to a greater extent, common (67%) species diversity models and it showed a negative relationship with both (Table 2). Longitude also showed a negative relationship with both (i.e. decreased diversity towards the east) and contributed 12% and 11% to common and rare richness models, respectively. Meanwhile, the dominant predictors with positive relationships to species richness were standard deviation in slope (22%) and pit landform coverage (13%), for rare and common diversity, respectively, while the second most important were basic soil parent material coverage (17%) and river length (8%). Links between hydrology and rare species richness were virtually non-existent, except when the northern area was assessed in isolation. The combined contribution from dominant mineral coverage data for rare species diversity across the whole of the Cairngorms was approximately 25%, and this was from a positive relationship with richness.

Table 2 Key species richness results (% model contribution) from the models using dominant mineral in the soil parent material. Full results are in Appendix S3. The common species richness model only had four predictors following simplification (see methods). Elev. = elevation.

	Common Species Diversity (SS = 43; CV = 36)		**Rare Species Diversity** (SS = 58; CV = 38)	
	Positive	Negative	Positive	Negative
Predictor 1	Forms – Pit (13.28%)	Elev. (mean) (-66.65%)	Slope (SD) (22.10%)	Elev. (mean) (-13.40%)
Predictor 2	River Length (7.66%)	Longitude (-12.41%)	Soil – Basic (17.08%)	Longitude (-10.98%)
Predictor 3	NA	NA	Forms – Hollow (15.29%)	Elev. (SD) (-8.09%)

Table 3 The frequency of dominant model predictors with either positive or negative relationships with species' distributions. Structure: predictor (count, average model contribution as a %), where 'count' is the number of times that a predictor was the main predictor in the species' distribution models ('SDMs'). Results are shown for common and rare distribution models across the whole study area when either soil parent material (PM) mineralogy (a) or texture (b) was used. A full table of results containing each species and the top five positive and negative predictors, as well as the model fit statistics and pivot tables, is provided in Appendix S3. If there was a joint ranking for position number 5 (i.e. two predictors were dominant in the same number of models), then the one with the greatest average contribution was used. Abbreviations: Elev = elevation; SD = standard deviation; Soil = soil parent material according to whether dominant mineral (a) or texture (b); LS = light-sandy; CS = clay silica; HM = heavy and medium

		(a) Soil Parent Material (PM) Dominant Mineral models		**(b) Soil Parent Material (PM) Texture models**	
Most dominant POSITIVE model predictors		**Common SDMs (n = 565)**	**Rare SDMs (n = 113)**	**Common SDMs (n = 558)**	**Rare SDMs (n = 116)**
	1	Forms – Pit (102, 20.51%)	Elev (mean) (20, 41.80%)	Forms – Pit (118, 19.66%)	Elev (mean) (20, 42.25%)
	2	Longitude (93, 22.26%)	Longitude (14, 26.48%)	Longitude (104, 21.80%)	Longitude (15, 31.63%)
	3	Slope (SD) (52, 20.46%)	Soil – $CaCO_3$ (7, 39.85%)	Slope (SD) (53, 20.12%)	Slope (SD) (13, 28.46%)
	4	Soil– Silica Clay (49, 20.17%)	Slope (SD) (7, 39.48%)	River Length (45, 18.29%)	Soil – HM (13, 26.07%)
	5	River Length (44, 19.19%)	Forms – Pit (7, 17.33%)	Soil– Light Sandy (37, 21.21%)	Soil – LS (9, 24.23%)
Most dominant NEGATIVE model predictors		**Common SDMs (n = 565)**	**Rare SDMs (n = 113)**	**Common SDMs (n = 558)**	**Rare SDMs (n = 116)**
	1	Elev (mean) (408, -32.55%)	Elev (mean) (29, -32.08%)	Elev (mean) (403, -33.30%)	Elev (mean) (35, -32.20%)
	2	Longitude (50, -18.44%)	Longitude (20, -22.89%)	Longitude (50, -19.68%)	Longitude (22, -22.78%)
	3	Elev (SD) (27, -24.62%)	Forms – Slope (7, -13.22%)	Elev (SD) (35, -22.34%)	Forms – Slope (9, -12.41%)
	4	Forms – Hollow (9, -16.39%)	Soil – Acid (5, -13.20%)	Forms – Hollow (9, -17.27%)	Elev (SD) (5, -14.74%)
	5	Slope (mean) (7, -20.11%)	Slope (mean) (4, -12.69%)	Forms – Valley (8, -15.03%)	Forms – Pit (3, -20.15%)

Models of species' distributions using either soil PM texture or dominant mineral, the most frequent dominant predictors (i.e. those with the highest model contribution) were generally consistent between one another and the soil PM parameter used made little difference on the overall model results (Table 3). Dominant predictors with a positive relationship with common species' distributions included (in decreasing order): pit landforms, longitude, slope (standard deviation), river length, and soil PM (either silica clay as the dominant mineral, or light-sandy for textures). For rare species, positive dominant predictors included: mean elevation, longitude, slope standard deviation, and various soil PM attributes, including those seen for common species as well as calcium carbonate dominant mineral coverage. Dominant negative predictors were similar between common and rare distributions, including: mean and standard deviation in elevation, mean slope, and longitude. Mean elevation and longitude were strongly related to some species' distributions positively and some negatively.

Specifically, soils with a PM with a clay-silica minerology (e.g. *Eriophorum latifolium*, *Papaver dubium s.s.* and *Sanicula europaea* all had model contributions of > 25% for clay-silica as the dominant PM Mineral) and light-sandy (e.g. *Pilosella aurantiaca*, *Arctium minus*, and *Verbascum thapsus* had model contributions of > 35% for light-sandy as the PM texture) or heavy-medium (e.g. *Euphrasia scottica* [negative] and *Potamogeton obtusifolius* each had model contributions of > 35% for light-sandy as the PM texture) textures were particularly informative for common species' distributions. Meanwhile the presence of calcium carbonate (e.g. *Juncus alpinoarticulatus* [negative], *Carex capillaris* [negative], and *Alchemilla wichurae* each had model contributions of > 40% for light-sandy as the PM texture) was additionally important for rare species. These species represent just a few examples: results are detailed for each species in Appendix S3.

All models performed reasonably well, particularly for rare species, with self-statistics (SS) repeatedly greater than 50 (out of 100) (Fig. 3). Most patterns seen for the whole Cairngorms National Park were broadly reflected in the north, east, south, and west individually. Longitude was regularly the most dominant individual variable with a median of approximately 15% for rare and common species diversity and distributions (i.e. patterns). The combined contribution from topography was consistently highest, and more so for rare species, but the directionality of the relationship between species' distributions and topography showed much variation from one species to another. The addition of geodiversity consistently and significantly improved the species richness and species' distribution models, with broadly positive relationships with species' distributions and species richness (Table 4).

Table 4 The mean and maximum model fit (SS) and evaluation (CV) difference (diff.) after the addition of geodiversity. The significance of differences were calculated using a paired Mann–Whitney U test of model statistics before and after addition of GDCs. N.b. all BRT SS and CV statistics have been multiplied by 100 in this study (see methods). *p < 0.001.

	Common species' distributions		**Rare species' distributions**	
	Soil texture	**Soil mineralogy**	**Soil texture**	**Soil mineralogy**
SS diff. mean (max, SD)	5.2* (42.2, 10.4)	5.2* (47.1, 9.7)	4.6* (38.9, 11.7)	4.8* (39.3, 13.4)
CV diff. mean (max, SD)	2.2* (35.7, 5)	2.40* (291, 5.2)	3.3* (46.3, 9.9)	4.7* (43.2, 10)

Discussion

Previously recognised fine-scale relationships are detectable at macroecological and landscape scales, according to our findings, and considering individual geofeatures relating to landforms, hydrology, and soil parent material (PM) properties added to our knowledge of the relationship between geodiversity and rare (defined broadly) and common vegetation biodiversity and species' distribution patterns in an upland British landscape (aim i). Indeed, explicit links between rare species' distributions and land surface materials were highlighted in our analyses. Meanwhile, standard topography and climate-relevant predictors were often dominant in the models in terms of their contribution, with geodiversity having an additive rather than dominant effect. We also observed frequent model interactions between elevation, which is important for temperature, and longitude, which was included as a proxy for precipitation. Within the limited body of geodiversity work thus far, our findings support the role of geodiversity at the landscape scale and, specifically, for mountainous areas. Indeed, the overall contribution of geodiversity to rare and common species richness here was greater than the national median for native and alien species richness across Great Britain across many landscapes nationally (Bailey et al., 2017). To find that geodiversity is also important for rare and common species' distributions is a significant advancement.

Improved knowledge of species' relationships with specific geofeatures is likely to be important, whether it be due to a direct or indirect relationship. Indeed, even for species whose modelled distributions were dominated by climate, geofeatures often showed additive effects. Those species for which geofeatures are seemingly most important may be safeguarded against climatic changes where geofeatures are managed appropriately. Indeed, the presence of specific materials (geology and soil), landforms, and hydrological systems may help to ensure

persistence and geodiversity has been linked to species' persistence and adaptation to climate change in the United States, for example (Albano, 2015). Meanwhile, for those species whose distributions are dominated by climate but where geofeatures were still contributory, indirect climatic effects are likely to be manifested within these features. For example, increases in monthly minimum temperatures are likely to affect species not only directly, but also via changes to geomorphological and soil processes, such as changes in weathering, erosion, disturbance events, and water storage and transfer (Brazier et al., 2012), and changes in microbial communities (Zogg et al., 1997). Many such processes are implicitly incorporated in our models through the explicit inclusion of geodiversity, which may act as a proxy for microclimate and fine-scale resource availability (Hjort et al., 2015; Tukiainen et al., 2017). In the context of future climate change, these findings may be of significance in understanding species' distribution changes considering the expected temperature and rainfall increases in this part of the United Kingdom (Werritty, 2002).

Mineral and nutrient availability should be important for biodiversity and species' distributions at the landscape scale and that is what we found here at the landscape scale, with differences between common and rare species (aim ii). Soil parent material (PM) is understandably very closely related to the topsoil within which the plants grow, and soils with dominant basic mineral compositions seemed to support a higher diversity of rare species in the Cairngorms, probably because of the increased availability of relevant resources. We also observed an interaction between this GDC and slope standard deviation, suggesting that a combination of topography and soil composition are important for rare species richness. Beyond overall diversity, the coverage of various soil PM properties was also useful for understanding rare species' distributions, whilst model contributions from hydrology and landforms were similarly important between common and rare species' distributions.

Some of the plants on the Cairngorms Rare Plant Register (RPR; see Amphlett, 2013), which itself defines rare species relatively broadly (see Methods), were of note within the results when scrutinising specific geofeature-species relationships. For example, we noted the importance of calcium carbonate as the dominant soil PM mineral for the models of distributions for *Alchemilla wichurae* (Rock Lady's mantle; defined as 'rare' within the Cairngorms; 60% model contribution from calcium carbonate PM coverage), *Carex capillaris* (Hair Sedge; a localised species within the Cairngorms; 51% model contribution), and *Juncus alpinoarticulatus* (Alpine rush; 'near scarce' within the Cairngorms; 45% model contribution), which all have a preference for basic, calcareous soils (Stace, 2003; BSBI, 2016).

Other dominant model predictors for the species mentioned above included slope coverage, mean slope, and clay-silica (60/40 clay/silica) soil PM coverage, which is an intuitive outcome considering that these species are usually found on mountain sides. These patterns have seldom been extrapolated to the macroecological scale, however, as is also the case for the other geofeatures in this study. Fine-scale data on microclimate and edaphic conditions do not always exist in places where management decisions have to be made, so the fact that some of the known local relationships between biodiversity and species' presences with geofeatures are detectable is of great potential value. It was not our aim to provide a species-by-species analysis here, but SDM results have been provided for every species (Supplementary S1).

Pit landform coverage (i.e. areas of depressed land surface surrounded by relatively flat ground) was frequently a dominant predictor that had a positive relationship with species' distributions This variable is likely to be hydrologically relevant and may represent unmapped lochans (small lakes), ponds, bogs, and river channels, for example. They will frequently be very moist and may form temporary ponds, which have been linked closely to species' distributions (Vandvik et al., 2005; Hjort et al., 2015). Interactions between river length and pits were also observed, which further points towards the hydrological relevance of pit landforms. They are, however, likely to be important beyond their hydrological properties because indented surfaces can provide protection from high winds, humans and grazing animals (Vandvik et al., 2005). This is where quantifying actual landforms becomes of great value compared to using crude DEM-derived metrics such as the topographic wetness index (TWI), for example. TWI (and similar metrics) may also fail to accurately represent hydrology and soil moisture levels effectively because of local edaphic and geological conditions. Similarly to pits, hollows, which are defined as a depression in the land surface surrounded by a slope (see Fig. 3 in Jasiewicz & Stepinski, 2013), provide sheltered environments with potentially unique abiotic properties. Hollows were important for the rare species diversity models and interacted with slope metrics (mean and standard deviation). Such landforms, which have been identified as important for overall species richness at the landscape scale elsewhere (Bailey et al., 2017), are also likely to aid in the persistence of snow patches and cooler conditions in montane environments via the provision of microclimates, higher moisture levels and the presence of unique soil resources, hydrologic and edaphic conditions (Litaor et al., 2008).

Our findings relate to the body of research on 'Conserving Nature's Stage', in which the focus of conservation is on the areas capable of supporting higher biodiversity, regardless of the changing climate, because of inherently higher geodiversity (Anderson and Ferree, 2010). Geodiverse locations are thought to improve species' ability to adapt and persist in the face of climatic changes (Albano, 2015). As we have shown here, however, there are clear differences

regarding the importance of specific geofeatures, and we would urge caution with overall geodiversity metrics because they may overlook useful information of individual landforms and surface materials. Indeed, our soil parent material diversity metric was seldom of greater value than knowledge of individual landform and land surface materials' coverage. An overall geodiversity metric may identify an area as a good 'stage' upon which to conserve biodiversity but give no information as to why that site is good, beyond that it is 'geodiverse': hydrological features, a certain soil type, or specific landform might be driving the richness-geodiversity relationship and targeting this/these feature/s is likely to be of value to management efforts. Therefore, any geodiversity metrics should, where possible, be accompanied with geofeature-specific analyses. Where data exist, we would also do well to consider existing species distributions in suitable 'stages' as well as biodiversity. This would be beneficial scientifically, as well as for practical conservation.

Grazing, especially from deer and hare, is of particular relevance to management in Scotland and for British uplands more widely. It is not possible without fine-scale ecological studies to ascertain the extent to which certain landforms (e.g. depressions such as pits and hollows) have contributed to our models in relation to the prevention of grazing. However, previous work suggests that some landforms can indeed protect plants, bryophytes and lichens from grazing (e.g. Gulliver, 2013; Moore & Crawley, 2014), and it is likely that the landform-species relationships that we have noted at the macroecological scales in this study are at least partly a reflection of this. Deer numbers in Scotland are thought to be stabilising after sharp increases since the 1960s, however, deer numbers are actively being reduced in some parts of the Scottish Highlands (Edwards & Kenyon, 2013), with some areas completely fenced off. These areas could reveal much about the ability of landforms to shelter species from herbivores. For example: how do geofeature-biodiversity and geofeature-species relationships differ between grazed and ungrazed areas? Disentangling and relating the influence of landforms and other geofeatures on species' distributions via the abiotic (e.g. microclimates, resource variety, sheltering) and the biotic (e.g. grazing, competition, dispersal) should be a future focus.

Data produced using geomorphometry were of great value in this study. These data required nothing more than a relatively fine-scale DEM and open source GIS software (GRASS GIS). Such techniques will no doubt become more common as algorithms develop and the user base of open source GIS software expands. Such techniques open up the potential to quantify landforms across large areas, which would be expensive and time-consuming to map accurately in traditional ways. However, whether explicitly mapped landforms or automatically-extracted landforms (e.g. as used in Hjort et al., 2012) are of greater use in the

context of biodiversity and species' distribution modelling remains an open question. We also used some very detailed, expertly produced datasets, from which geophysical properties (e.g. soil parent material mineralogy and texture) were quantified across our study area. These data may be harder to extract automatically, but remote sensing techniques have much potential in this context (see Bailey et al., 2017).

Our study represents a clear progression of the use of geodiversity within the broader body of environmental heterogeneity research by analysing geofeatures in relation to rare and common species' distributions and richness in a sensitive upland landscape. A greater awareness of geofeatures in conservation and management may be beneficial in the face of environmental change and future work may wish to explicitly focus on developing these geodiversity data for use in that arena. Species-by-species assessments could also make greater use of geofeature information. Whilst the Cairngorms, along with the rest of the UK, is well mapped, the explicit mapping of landforms remains patchy and definitions are inconsistent: automated landform extraction techniques are therefore of great potential value from a management point of view, perhaps as a first pass over an area to enable identification of sites for further study in the field. Ultimately in the context of this study, we have demonstrated the value of geodiversity in enhancing our understanding of patterns of life. Identifying when and where different geodiversity is of the greatest value, and for which taxa, should be a primary research focus moving forwards.

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Supporting Information

Appendix S1: Hydrology of the Cairngorms National Park

Appendix S2: Further information on the Cairngorms National Park

Appendix S3 (caption): Excel file containing detailed results **

Appendix S4 (caption): Full versions of Figure 3 **

Appendix S5 (caption): As S4, but for models using soil PM texture **

Author Contributions

All authors contributed strongly to the design of this research. JJB gathered and processed the data, conducted the analyses and drafted the manuscript.

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PAPER V: RELATING GEODIVERSITY TO SPECIES' DISTRIBUTIONS AND CROSS-SCALE PRODUCTIVITY IN AN UPLAND RIVER CATCHMENT

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Abstract

Aims Geodiversity, a characteristic of environmental heterogeneity, which relates to land surface materials (i.e. the substrate) and geofeatures (hydrological and terrestrial landforms), may relate to species' distributions and productivity via the provision of abiotic resources and niche space. However, the relationship between geodiversity and patterns of life remains understudied, especially in relation to the spatial scales at which various types of geodiversity data are useful. We therefore study geodiversity in relation to (i) species' distributions and (ii) spatial patterns of productivity. By studying these phenomena in parallel, we can substantially improve our understanding of patterns of life in relation to geodiversity at the landscape and local scales.

Methods We used geodiversity data alongside more widely-used topographic metrics (e.g. elevation, slope) to model (i) plot-scale vegetation occurrences for 82 species and (ii) productivity across an upland river catchment in the Central Scottish Highlands. The plot-scale data plant data included: angiosperms, conifers, fungi, lichens, liverworts, lycophytes, mosses, and pteridophytes for 283 100 m^2 sampling plots. Productivity was measured using NDVI, which was derived from 50cm colour infrared (CIR) aerial photography. It provides a consistent vegetation productivity metric, which we analysed across multiple scales (grain sizes from 625 m^2 to 40,000 m^2). Geodiversity and geofeature data were derived from digital elevation models and existing expertly-produced datasets, including the use of geomorphometry to automatically extract explicit landform data. The area of interest is a data rich upland river catchment that is representative of the wider area, meaning that patterns found are generalisable in this environment.

Results Geodiversity data relating to landforms, hydrology, and land surface materials made noteworthy contributions throughout our analyses (especially landforms), supporting the need for their incorporation and the effort required to generate these data. Traditional topographic predictors (especially mean elevation) dominated and explained most of the variance in species' distributions and productivity. We successfully linked individual species' distributions to specific geofeatures and these links were explicable and in line with species' known ecology. For productivity, landforms (ridges and spurs) contributed towards highlighting low productivity areas, whilst streams clearly and consistently related to higher productivity. Streams and certain landforms related to elevation, but also made unique model contributions.

Conclusions Landform data derived from digital elevation models and data on surface materials were helpful at the plot scale and were directly related to specific species' distributions, thus progressing our knowledge of how individual geofeatures relate to the biotic environment across in upland landscape. However, finer-scale geodiversity collected in the field might have added further. Our results may be especially important in the context of planning under future climatic change when geomorphological and geological processes directly and indirectly promote biotic shifts. We hope that this study will pave the way for more fine-scale geodiversity studies in ecology to test the geographical ubiquity of the patterns found here, developing on previous work to understand the links between geodiversity and patterns of life across scales.

Introduction

At large spatial extents, it has been consistently demonstrated that climatic factors are closely related to patterns of life on Earth (Field et al. 2009). When we consider spatial patterns in smaller areas, however, abiotic heterogeneity (Stein 2014) and biotic interactions (McGill 2010) become increasingly important in explaining species diversity and individual species' distributions (Valdés et al. 2015; Field et al. 2009). Our ability to manage species, biodiversity, and ecosystem services, is dependent upon having a sound understanding of patterns of life and the scales at which different correlates and mechanisms might be important (Gordon & Barron 2013).

A relatively recent advancement in the area of research into the role of abiotic heterogeneity has been that of 'geodiversity' (Gray 2013), which describes "the diversity of abiotic terrestrial and hydrological nature, comprising earth surface materials and landforms" (Fig. 1 in Bailey et al. 2017). Geodiversity necessitates the explicit quantification of geofeatures (e.g. landforms, geological types), unlike widely-used topographic metrics, which are conceptually separate. Such topographic metrics (e.g. range in elevation and slope; topographic openness) provide a crude quantification of the landscape which, whilst still having significant value, may miss important dimensions of the abiotic environment (Bailey et al. 2017; Tukiainen, Bailey, et al. 2017; Hjort et al. 2012). This is especially apt considering predicted changes in the geophysical environment under future climatic changes (Brazier et al. 2012; Hulme et al. 2002). Indeed, the geophysical environment may be an important determinant of biotic patterns and therefore requires more explicit consideration in ecological research (Albano 2015).

Individual geofeatures (e.g. a hollow in a mountainside) should theoretically relate to patterns of life via a number of ecological mechanisms and explicitly measuring landforms should allow us to implicitly capture these abiotic processes and conditions. These may include, for example: resources such as nutrients, water, and light; habitat diversity; microclimatic and sheltering effects; and soil moisture, texture and pH (Lawler et al. 2015; Hjort et al. 2015; Beier et al. 2015; Dufour et al. 2006; Keith 2011; Moser et al. 2005) (also see PAPER I). pH may be especially important in determining vegetation patterns and species diversity, as shown in arctic environments (Walker 2000; Gough et al. 2000; Ross et al. 2012). In turn, these abiotic factors should relate to niche availability and breadth. Disturbance events are also very likely to relate to plant species' distributions via alterations to fine-scale biotic interactions and biomass and changes in resource availability (Le Roux et al. 2013; Viles et al. 2008; Virtanen et al. 2010).

These theorised geofeature-species relationships seem to be detectable at macroecological scales according to the one cross-scale study conducted in this area so far. This study (in which the smallest grain size and extent were 1 km^2 and 25 km diameter, respectively) took place across the whole of Great Britain and quantitatively demonstrated that geodiversity data were useful at multiple scales (Bailey et al. 2017). However, these geodiversity data made the greatest contribution to native and alien plant biodiversity models at the landscape extent and for a grain size of 1km^2 (the finest scales in this study), with climate dominating at broader scales. Data on valleys, hollows, and other landforms were of the utmost importance. However, this was the finest scale in this study and, compared to plot-based ecology, the scales were still relatively coarse, leaving open questions about the role of geodiversity data at finer scales.

Elsewhere, rare and common plant species' distributions seem to relate to various geofeatures (e.g. certain geological types and landforms) at the landscape scale across the Cairngorms in the Central Scottish Highlands (PAPER IV). Similar relationships between geodiversity and patterns of life have also been shown within (Hjort et al. 2012) and across (Tukiainen, Bailey, et al. 2017) Finland, in a quarry in France (Bétard 2013), in the south-west USA (Albano 2015), in Switzerland (Dufour et al. 2006), and in tropical environments (Guitet et al. 2015), indicating some generality of these relationships (see review on geodiversity in conservation by Anderson et al. 2015). The importance of geodiversity and local abiotic factors has also been highlighted in relation to refugia (Lenoir et al. 2016; Gill et al. 2015) and the role of geodiversity in conservation biology is growing; see 'Conserving Nature's Stage' (Anderson & Ferree 2010; Beier et al. 2015; Tukiainen, Bailey, et al. 2017).

Our knowledge regarding the spatial scales and geographic locations where geodiversity is most useful has, therefore, advanced in recent years, but much remains to be done across scales, places, and taxa. The ecological limits also remain understudied: e.g. is geodiversity more useful for understanding overall biodiversity or species distributions?; which facets of biodiversity are most closely related to geodiversity?; are these data able to help us better understand overall ecosystem productivity?; in which environments are these data most strongly related to patterns of life? In line with two of these questions, there are significant gains to be made from aligning findings on individual plant species' distributions at the plot scale and overall cross-scale productivity in the same location. Indeed, as far as we are aware, no research thus far has studied productivity in relation to geodiversity.

Geodiversity is understudied beyond biodiversity and species' distributions. Though contentious, there is a generally accepted relationship between productivity and species richness, which relates to resource availability (Šímová & Storch 2016). Productivity has also been described as an intermediary between climate and diversity, possibly via water-energy dynamics (Lavers & Field 2006). Theoretically, geodiversity should therefore also relate to ecosystem productivity and spatio-temporal heterogeneity of productivity via the provision and variety of resources made available by geofeatures (e.g. Wen et al. 2012). Topography metrics relating to radiation and elevation have been previously linked to productivity (and biomass) in high latitude environments (Riihimäki et al. 2017; Boelman et al. 2003). Whilst explicit geofeatures were not considered by Riihimäki et al., their work supported the existence of a relationship between productivity and the geophysical environment, largely via abiotic resource availability.

Whilst productivity metrics are relatively easily obtainable, there are few places where high quality species' distribution data exist to afford insight into the limits of geodiversity data, but in this paper we have an area of interest which allows us to investigate some of these ideas with rich data. The site is also broadly representative of the wider landscape in the Scottish Central Highlands (and beyond), thus making any relationships found generalisable to the broader area. Such environments are expected to change substantially in the future (Brazier et al. 2012; Morrocco et al. 2016), yet they have also been identified as places that will be able to support biodiversity as the climate changes (Albano 2015; Lawler et al. 2015). A better understanding of the biota of mountainous, geodiverse areas is essential if we are to plan successfully for conservation and management going forwards.

We therefore present a two-part analysis focussing on an upland river catchment. (i) The first part aimed to assess the relationships between geofeatures and individual species'

distributions, using plot-scale data for 82 plant species across the study area. We predicted that certain landforms and geological types would be closely related to the distributions of many species at this scale, given the theoretical ecological links outlined above. The second analysis (ii) related productivity, as measured by the mean and standard deviation of NDVI derived from 50 cm resolution aerial colour infrared (CIR) imagery, to a similar group of geofeatures for the same site. Analysis (ii) used several grids with varying grain size to additionally assess the effect of spatial scale on the relationship between productivity and geofeatures. For both analyses, we expected geodiversity to make small (relative to topography data on elevation and slope) but consistent contributions to the models, as has been found elsewhere at coarser different scales (Tukiainen, Bailey, et al. 2017; Bailey et al. 2017).

Materials and Methods

Study area

The study area lies in the western half of Cairngorms National Park, within the Central Scottish Highlands, and it is focussed around, but exceeds slightly beyond, Invereshie and Inshriach National Nature Reserve (NNR) and the Allt a'Mharcaidh river catchment (CEH, 2017[1]; Fig. 1). The site is underlain by granite bedrock (the Cairngorm pluton) and has a climate typical of the Scottish Highlands: cool temperatures and frequent precipitation throughout the year, with temperatures below freezing in winter. Fauna at the site include: pine marten, red squirrel, red deer, mountain hare, and various species of bird, including the ptarmigan, red grouse and golden eagle. Meanwhile, the floral communities include pine forest in the lower part of the site (*Pinus sylvestris*) and heathland throughout much of the area interspersed with vascular plants and bryophytes. Bare ground is not uncommon on exposed ridges, whilst wet, peaty areas exist closer to the stream and in small pits and depressions throughout the site. In places, snow patches may last through to mid-summer (Fig 1.ii), with the entire site typically being covered by snow at some point during the winter. The elevation above sea level ranges from approximately 269 to 1108 m, with a mean of 694 (standard deviation = 161), whilst the slope ranges from 0 to 66° (mean = 17; standard deviation = 7.5). The total study area is 19.29 km^2 (1929 hectares).

[1] http://www.ceh.ac.uk/our-science/monitoring-site/invereshie-and-inshriach-nnr-cairngorms

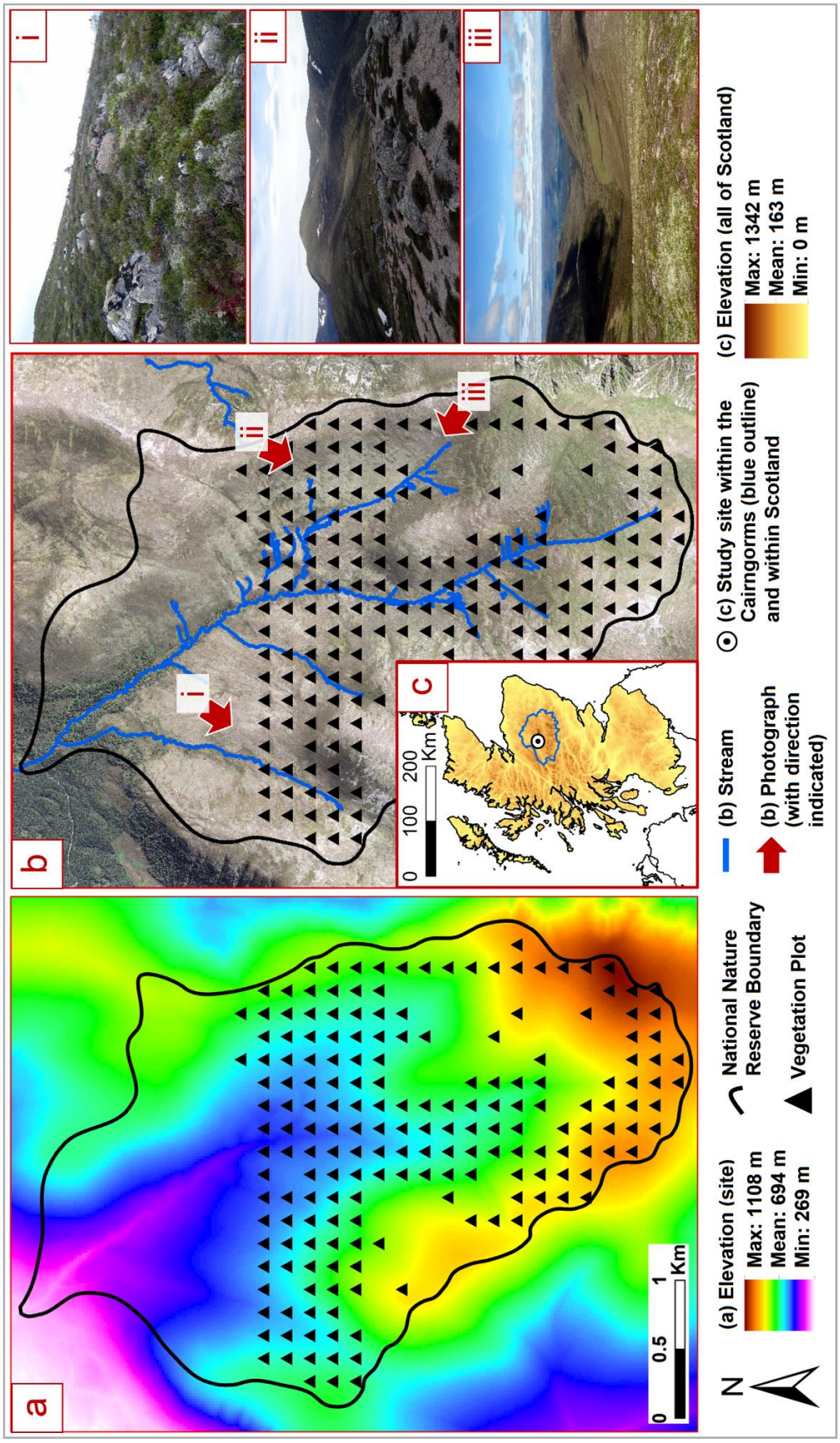


Figure 1 Study site details, including an elevation map (a) and aerial photograph (b) of the site, overlain by vegetation plot locations and stream locations. The context within Scotland is shown (c) Photographs © Joseph J. Bailey (taken in June 2014).

Data and Analysis

Data processing and analysis for the (i) plot-scale and (ii) cross-scale grid-based analyses were largely identical. Predictors of (i) species' distributions and (ii) NDVI fall into either 'topography' or 'geodiversity' (Table 1) and data were drawn from a wide variety of secondary sources. Topography data were derived from a 5x5 m resolution NEXTMap digital elevation model (DEM) and include: aspect ('northness'); elevation (mean and standard deviation) and slope (mean and standard deviation). NEXTMap data were obtained from Intermap via NERC Earth Observation Data Centre (NEODC). All spatial processing was done in ArcMap and data processing and analyses in R 3.2.0 (R Core Team 2017), unless otherwise stated.

Table 1 Geodiversity data: geofeatures, geodiversity components (GDCs), and data sources.

[1] https://www.ordnancesurvey.co.uk/business-and-government/products/os-open-rivers.html
[2] http://gateway.snh.gov.uk/natural-spaces/index.jsp (Contains Ordnance Survey data © Crown copyright and database right (2017));
[3] http://www.getmapping.com/;
[4] http://www.intermap.com/data/nextmap;
[5] Licence no. 2014/128 ED British Geological Survey VC NERC. All rights reserved.

Geofeature	GDC (measured geofeature)	Notes / Source
River / Stream	Distance from river	Obtained via Ordnance Survey Open Rivers[1,2] and enhanced through digitisation from 25 cm aerial photography, which was purchased from GetMapping[3].
Landforms	Areal coverage of each landform	r.geomorphon algorithm (Jasiewicz & Stepinski 2013) executed in GRASS GIS 7.1 (GRASS Development Team 2017) using 5 m resolution NEXTMap[4] DEM.
Geomorphological Type	Areal coverage of each type	Location and extent of the main landform assemblages. Copyright Scottish Natural Heritage[2]. Raster resolution = 12.5 x 12.5 m.
Soil parent material (PM)	Areal coverage of each type	British Geological Survey data under academic license[5]. Mapping scale: 1:10,000.
Superficial Deposit	Areal coverage of each type	British Geological Survey data under academic license[5]. Mapping scale: 1:50,000.

Geodiversity data

In line with previous work (Bailey et al. 2017), we use the term 'geodiversity component' (GDC) to refer to a measured geofeature (e.g. the areal coverage of a landform or geological type, or distance from a river). GDCs necessarily vary substantially between studies because of aims and data availability. The GDCs used herein are listed in Table 1 and include: geomorphological type, soil parent material and superficial deposit coverage, distance from nearest stream/river,

and landform coverage. The advantage of using the distance from an explicitly mapped river over the topographic wetness index (TWI) is that the presence of the rivers is a certainty because they are accurately mapped. However, the presence of a certain level of wetness is not because TWI accounts only for topography and not other local factors that affect wetness such as soil and permeability (Kopecký & Čížková 2010). This GDC is therefore still related to an explicit geofeature. We extracted landform data on peaks, ridges, hollows, valleys, spurs, pits, and slopes from the DEM using the r.geomorphon algorithm (Jasiewicz & Stepinski 2013; see Fig. 2) in GRASS GIS 7.1 (GRASS Development Team 2017), as in Bailey et al. (2017).

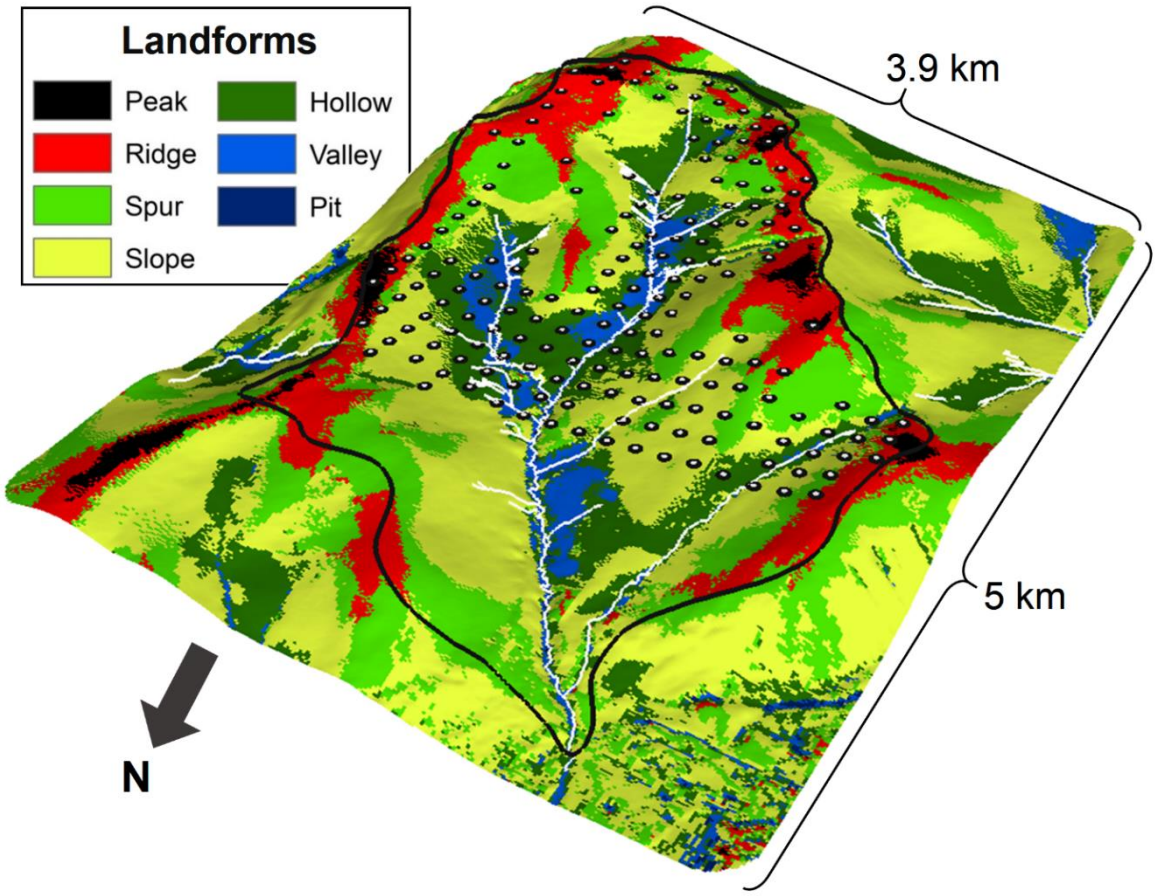


Figure 2 Geomorphon landform geofeatures across the site, looking south south-east. Streams (white lines) and vegetation plots (black circles with white dot in centre) are also shown. The 3D image was produced in ArcScene.

Plot-scale vegetation data (i)

The river catchment within which the vegetation plots exist is 10.51 km^2 (1,051 ha). There were 283 10 x 10 m vegetation plots, the data for which were aggregated from smaller plots (40 x 40 cm and 2 x 2 m) therein (sampling protocols are defined by the Environmental Change

Network [ECN][2]). Topography and geodiversity data were averaged within a 10 x 10 m square around the centroid of each plot and extending 2 meters beyond the edge of the plot, so as to ensure that the immediate geophysical environment was accurately represented in the data. Note that one of the variables was related to the distance from the nearest stream, so therefore the proximity of a stream is considered even if there was not a stream within the measured area. Vegetation data were collected by between 1998 and 2014. A presence absence matrix was produced that included the following taxa: angiosperms (n = 28), mosses (22), lichens (17), liverworts (6), fungi (4), lycophytes (3), conifer (1), and pteridophytes (1; total number of species = 82).

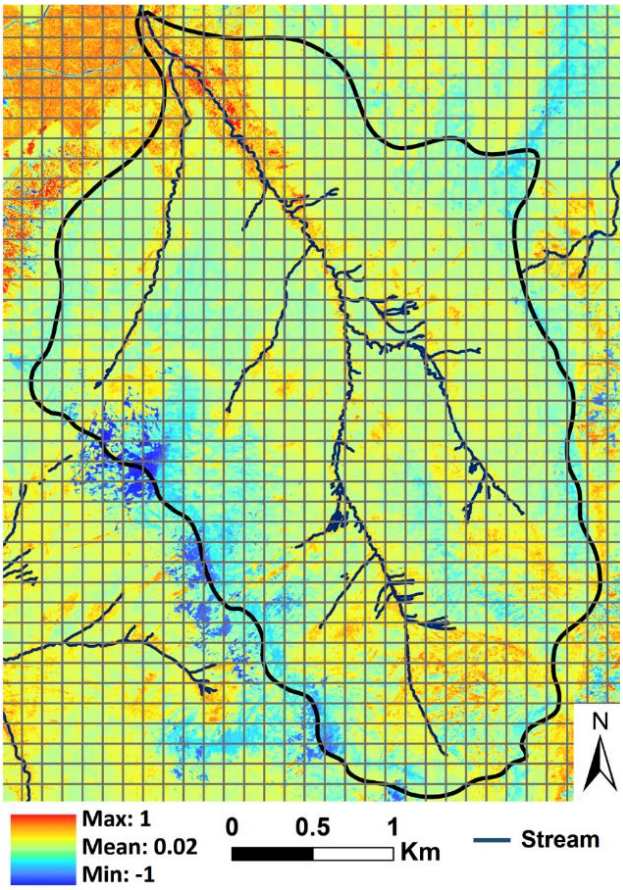


Figure 3 Normalised difference vegetation index (NDVI) across the site, overlain by the 125 x 125 m grid.

Productivity (NDVI) data (ii)

Analysis (ii) extends slightly beyond the edges of the river catchment and National Nature Reserve (Fig. 3). A proxy for relative primary productivity, ranging from -1 to +1 across the landscape, was measured via computation of the Normalised Difference Vegetation Index (NDVI), a metric which tracks variation in photosynthetic capacity. NDVI was derived from 50 cm resolution colour infrared (CIR) aerial photography (orthorectified RMSE +/- 1m) in ERDAS IMAGINE 2016. These data were captured by Getmapping®[3] on July 19th (2013), which coincides with peak vegetation productivity in this area.

NDVI is based on the ratio between low reflectance (absorption) of radiation by chlorophyll at red (R) wavelengths and high reflectance by plant cells of the near-infrared

[2] http://www.ecn.ac.uk/measurements/terrestrial/v
[3] http://www.getmapping.com/

(NIR) wavelengths (Virtanen et al. 2010; Wen et al. 2012). It is calculated as follows: (NIR - R)/(NIR + R). The mean (productivity) and standard deviation (to represent the variation in productivity within the grid cell or vegetation plot) of NDVI was calculated per grid cell across several grain sizes (grid cell sizes) to study the effect of spatial scale (Table 2). The total area within which the grids fell was 17.3 km^2 (1,738 ha) but some of the grids did not cover this whole area because of geometric constrains. Grid cells that had less than area within the defined study (Fig. 1) area where the full abiotic datasets existed were removed from the analysis.

Table 2 The number of grid cells in each grid for NDVI analyses.

Cell size (m)	Number of cells
200 x 200	303
175 x 175	379
150 x 150	506
125 x 125	713
100 x 100	1,082
75 x 75	1,858
50 x 50	4,047
25 x 25	15,623

Analysis

Boosted regression trees (BRTs, a machine learning technique), were used to model species richness in R 3.2.0 (R Core Team 2017; Elith et al. 2008). BRTs deal with collinearity, non-linearity, and interactions well (Dormann et al. 2013). Specifically, we used gbm.step in the gbm 2.1.1 package (Ridgeway 2017). For analyses of vegetation plot data (i), each species' occurrence was used as the response, whilst in the productivity analyses (ii), the mean and standard deviation in NDVI were used. BRTs are capable of having a binary or continuous variable as the response, so suited our purposes well and allowed for comparative results between species' distribution and productivity models. Specific parameters for the BRTs included: maximum tree complexity of 3 and a learning rate of at least 0.01 (reduced if model failed). The relative influence (model contribution) of each predictor is reported as a percentage and self-statistics (SS; internal fit) and cross-validation (CV) statistics provided (Ridgeway 2017; Elith & Leathwick 2011).

Results

Plot-scale vegetation data

Mean elevation contributed greatly to plot-scale models of species' distributions across all taxa, but the directionality of the relationship was highly variable (Fig. 4): e.g. model relative influence (RI) ranged from -79.6% (*Ptilium crista castrensis*; moss) through zero (*Cladonia carneola*; lichen), to 80.8% (*Carex bigelowii*; angiosperm), where a positive value indicates increased presences of a species in higher elevation plots. At a coarser taxonomic level, the RI

of mean elevation was strongest for liverworts, lichens, and lycophytes, which almost consistently increased in occurrence with increasing elevation; fungi, mosses, pteridophytes, and conifers were typically found at lower elevations, while angiosperms were quite mixed. Of other topographic predictors, which were of much less importance in the models than was mean elevation, mean slope was positively related to most angiosperms, liverworts, pteridophytes, and lycophytes; the RI and directionality of the standard deviation in slope and elevation were mixed. Elevation standard deviation was especially relevant for pteridophytes (positive relationship). Angiosperms, mosses, liverworts, pteridophytes, and lycophytes were more commonly found in north-facing plots and fungi, lichens, and confiders in south-facing plots but, again, results were mixed within and between taxa for aspect.

Of the geodiversity predictors (distance from hydrological feature, landforms and land surface material coverage), results were also very mixed. Landform coverage data had a non-zero influence in BRT models for 38 species out of 82 (26%). In these 38 models, landforms had a consistent additive effect and the relationship between landforms and species' occurrences was almost exclusively positive (i.e. increase in these landforms correlates to increased occurrence of a given species). The highest contribution from landforms was the presence of slope for *Cladonia crispata* (33.79%; lichen). Other examples include: the coverage of hollows for *Loiseleuria procumbens* (22.68%; angiosperm – dwarf shrub); ridges for *Cladonia fimbriata* (25.79%; lichen); slopes for *Diphasium alpinum* (29.83%; lycophyte); and spurs for *Cornicularia sp*. (15.74%; fungi). Peaks and pits were never of any relevance here. Geomorphological type, soil parent material (PM), and superficial deposit also made consistent positive contributions to models for the species within angiosperms, fungi, mosses, liverworts, and lichens (i.e. not pteridophytes, lycophytes, and conifers) where RI was non-zero.

Models generally had a very good internal fit (mean of 0.70 out of 1; min = 0.47; max = 0.95; standard deviation = 0.11) but cross-validation statistics were weaker (mean = 0.31; min = 0.04 max = 0.77; standard deviation = 0.17). Meanwhile, the most frequent and dominant interactions were between various topographic measures (i.e. involving aspects, slope, and elevation), with strong model interactions between geodiversity predictors far less common (Table 3).

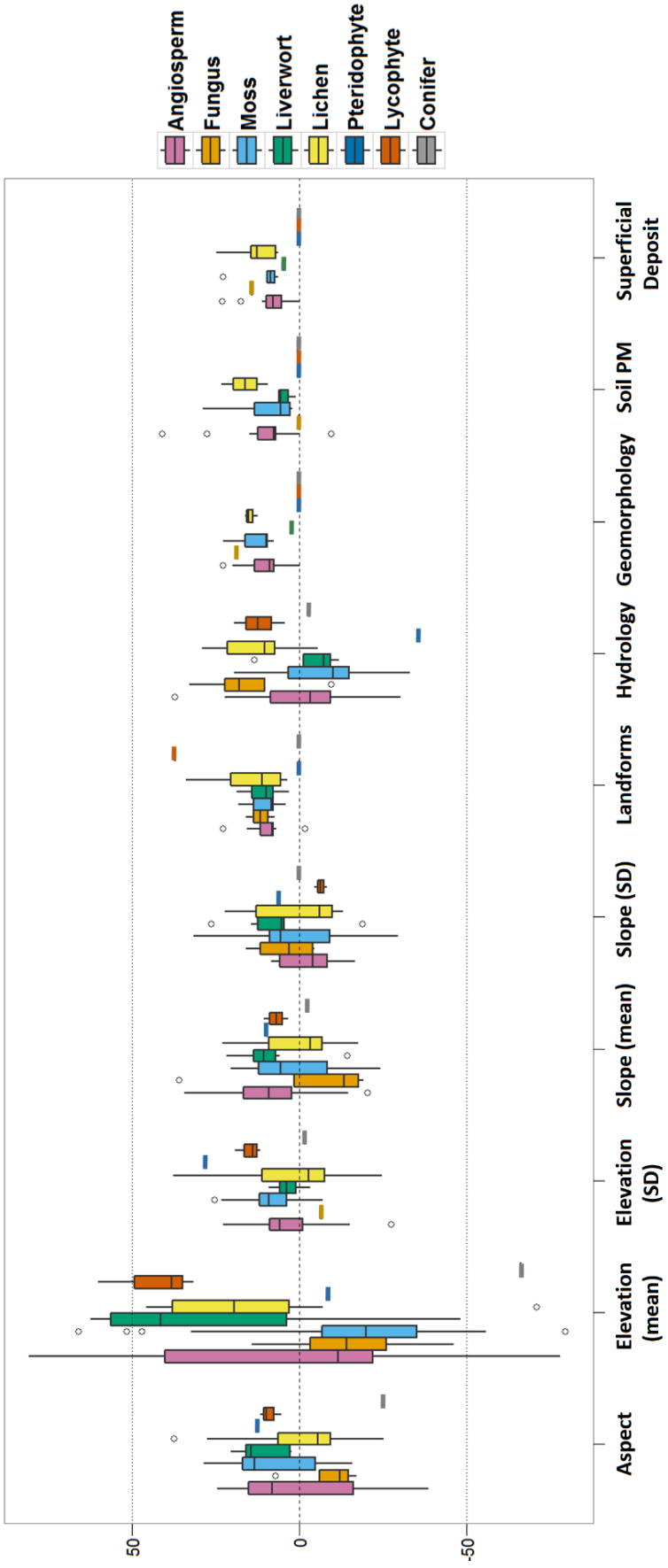


Figure 4 The model contribution (relative influence; %) of each predictor or set of predictors on plot-scale species' distributions for each species group, as determined by BRT modelling. Angiosperms (n = 28), mosses (22), lichens (17), liverworts (6), fungi (4), lycophytes (3), conifer (1), and pteridophytes (1); total number of species = 82. Where no box is shown and only a line (e.g. all conifers), there was only one species for that species group result.

Table 3(caption overleaf)

	Scale	SS corr-elation	CV corr-elation (mean of 10 folds)	**(i)** Relative Influence (%) of each predictor set (absolute value; no direction indicated) **(ii)** Individual predictors with relationship to response indicated					
				(i) Topo-graphy	**(i) Landforms (Geomorphon)**	**(i) Soil**	**(ii) River Distance**	**(ii) Main individual predictor**	**Dominant Model Interaction**
NDVI (mean)	**25 x 25 m**	0.84	0.78	64.87	15.11	0	-20.01	Elevation (-43.16)	River Dist * Elev
	50 x 50 m	0.90	0.80	63.84	16.24	0	-19.92	Elevation (-41.77)	River Dist * Elev
	75 x 75 m	0.92	0.82	57.27	17.36	5.10	-20.26	Elevation (-37.16)	River Dist * Elev
	100 x 100 m	0.94	0.80	56.78	18.77	6.75	-17.70	Elevation (-37.47)	Elev SD* Elev
	125 x 125 m	0.97	0.81	58.71	16.89	6.14	-18.26	Elevation (-36.88)	Slope * Elev
	150 x 150 m	0.96	0.80	47.34	20.45	10.42	-15.68	Elevation (-31.86)	Spur * Elev
	175 x 175 m	0.93	0.83	50.27	23.80	9.40	-10.12	Elevation (-39.15)	Elev SD* Elev
	200 x 200 m	0.97	0.82	56.11	9.31	0	-16.74	Elevation (-36.74)	Spur * Elev
NDVI (SD)	**25 x 25 m**	0.75	0.65	85.13	0	0	14.87	Elevation (+36.88)	Slope * Elev
	50 x 50 m	0.81	0.66	86.45	0	0	13.55	Elevation (+33.01)	Elev SD * Slope
	75 x 75 m	0.77	0.66	86.85	4.74	0	-8.41	Elevation (+35.81)	Slope * Elev
	100 x 100 m	0.79	0.66	91.29	0	0	-8.71	Elevation (+34.51)	Slope * Elev
	125 x 125 m	0.81	0.63	90.69	9.31	0	0	Elevation (+29.81)	Slope * Elev
	150 x 150 m	0.87	0.65	100	0	0	0	Elevation (+35.32)	Elev SD* Elev
	175 x 175 m	0.77	0.64	100	0	0	0	Elevation (+40.88)	Slope * Elev
	200 x 200 m	0.79	0.63	97.36	2.64	0	0	Elevation (+32.82)	Slope SD * Elev

Table 3 (previous page) NDVI results across all spatial scales (including plot scale) when all predictors were used. The influence of each predictor set on the BRT models is shown for each scale: the darkest shades indicate values over 50% and lighter shades between 10% and 50%. 'Hydrology' only refers to one predictor which is distance from stream, whilst all others are predictor sets. Superficial deposits and geomorphology types are not shown here and had model influence at the coarser scales for mean NDVI only: superficial deposits for 200 x 200m scale (10.7%) and geomorphology type for 150 x 150m (6.11%), 175 x 175m (6.40%), and 200 x 200m (7.14%). 'Slope' and 'Elevation' (or 'Elev') are always referring to the mean unless SD used to indicate standard deviation. SS = self-statistic; CV = cross-validation; SD = standard deviation; Dist = distance.

Productivity (NDVI): cross-scale analyses

Models of mean NDVI (our measure of productivity) had very high internal fits and high cross-validations scores, and those for standard deviation (SD) of NDVI (our measure of variation in productivity) were also reasonably high across all scales (Table 3). Topography dominated all of the models, with combined relative influence values usually exceeding 50% (max of 64.97% at the finest scale) for mean NDVI models and always exceeding 85% (at or close to 100% for the coarsest scales) for all NDVI SD models. Mean elevation was the most important predictor within topography but this predictor had a positive relationship with mean NDVI and a negative relationship with NDVI SD. Model interactions were always among topographic predictors or between topography and hydrology (river distance). Broadly speaking, the model relative influence values for topography diminished as spatial scale coarsened for mean NDVI and increased with coarsening scale for NDVI SD, essentially saturating at 100%.

Of the geodiversity variables, the model influence of landforms (from geomorphometry) for mean NDVI increased as the scale coarsened, up to the 175 x 175 m grain size, when it then decreased at the coarsest scale. Within the landforms, it was the ridges, spurs and less hollows that related to mean NDVI. Spurs were consistently negatively related to NDVI and ridges were positively related at the finest scales and negatively at 75 x 75 m and coarser. Hollows related positively to NDVI at the 150 x 150 m and 175 x 175 m scale. Model influences from landforms were typically in single figures (i.e. < 10 % model contribution). The distance from a river was also important and mean NDVI decreased as distance from a watercourse increased. Soil parent material was partially important for mean NDVI at some of the meso-scales. Geodiversity variables were typically not important for modelling NDVI SD, except for river distance at the finest scales, and landforms had a small model influence at the 125 x 125 m scale. Finally, we note that NDVI was also used as a response at the plot scale and results were comparable to the finest grain size in the grid-based analyses.

Discussion

Geodiversity data relating to landforms, hydrology, and land surface materials made noteworthy contributions throughout our analyses (especially landforms), supporting the value of their incorporation into ecological analyses and the effort required to generate these data. As expected, topography dominated most of the models of individual species' distributions and of NDVI, whereby mean and standard deviation of NDVI were used as proxies productivity and variation in productivity, respectively. Indeed, mean elevation was particularly important across most of our analyses. The dominance of elevation across is probably largely because of its general relationship with the weather cooler, windier conditions, which are normal at higher elevations in this environment, as is bare ground or thin soils because of these conditions (Wrightham & Kempe 2006; Gordon et al. 2006). The distance from a stream was frequently important as well, sometimes independently of, and also through interactions with, elevation, probably because of increased soil moisture levels nearer to a river, which, in turn, is likely to be affected by soil type (Geris et al. 2015). There were clear differences in the responses of (i) different species at the plot scale and for (ii) productivity (mean and standard deviation) across spatial scales in relation to topography and geodiversity predictors.

Analysis (i): plot scale

It is difficult to make broad taxonomic generalisations from this study's plot-scale analyses (analysis i) because of the relatively small number of species, but for the species groups studied, some clear patterns emerged in relation to geodiversity. For example, mosses, liverworts, and pteridophytes almost exclusively increased nearer to rivers (fungi and lichens decreased). Rivers are typically surrounded by moist soil, which is important for some species, but they can also provide a dynamic environment. In such environments, fine-scale disturbances are common and these may create space and suitable conditions for certain species across different taxa, contributing to this relationship. Indeed, geomorphological disturbances have been linked previously to species' distributions (Le Roux et al. 2013).

Landforms and land surface materials were consistently positively related to species' distributions and made relatively small (compared to elevation) but important contributions to our models across all most species groups. For *Diphasium alpinum*, a lycophyte, knowledge of the presence and coverage of slope landforms helped explain its distribution. These results are in line with the fact that it is often found in exposed locations (Stace 2010). *Cladonia fimbriata* is a common lichen, which was here related to ridges where exposed soils or bare

ground may provide a suitable habitat. *Cetraria nivalis* (lichen) was related to head deposits (poorly sorted deposits produced by slope processes) and *Sphagnum tenellum* (moss) to peat deposits, which is again in keeping with their known ecology of exposed rocks and moist and acidic conditions, respectively. *Loiseleuria procumbens* is known to favour rocky and boggy alpine or sub-alpine environments (typically found above the tree line) and here related strongly to hollow landforms and high elevations (Stace 2010). Indeed, the presence of peat was important for the distribution of other species associated with such conditions (e.g. *Cladonia polydactyla*, *Eriophorum angustifolium*). Hollows may be able to provide such moist conditions in places where the surrounding slope is unsuitable. Geomorphological mapping was also very useful. For example, glacial drift helped explain the distribution of *Cladonia carneola* (lichen) and solifluction sheets (periglacial) the distribution of *Rubus chamaemorus* (cloudberry). However, some surface materials were rarely or never of relevance to any species' distributions.

These species provide examples of how species-specific ecologies have been related to relatively fine-scale maps of superficial deposits and landforms. In line with our initial predictions, it seems that for many species, geofeatures represent an important set of predictors that can explain residual variance in species distribution data after topography, representing understudied dimensions of environmental heterogeneity. Geofeatures implicitly capture abiotic conditions (pH, moisture) and processes (e.g. disturbance, transport in rivers, sheltering and exposure). Limiting a study such as this to crude DEM-derived topographic variables would have missed much important information at the plot scale. For multiple species, the mapped head deposits, which are found at the bottom of slopes and result from disturbance processes on higher ground, were important. Geomorphological disturbance and short-term climatic changes (26 years) have been previously linked to high-latitude vegetation change (Virtanen et al. 2010). Comparative studies of such temporal change are rare and more are needed to reliably distinguish these relationships because factors that were not measured in Virtanen et al.'s study (e.g. grazing or insect population changes). This is especially so if we are to confirm direct and indirect relationships between climate change effects on vegetation communities via geofeatures (Brazier et al. 2012). Our dataset here did not allow for temporal analyses, but the clear geofeature-species links support the need for such future analyses.

Biotic interactions at our site are also of significance. Deer are present throughout this study area and landforms can act important refuges for some species, sheltering them not only from harsh abiotic conditions, but also from these grazing mammals. Interactions between grazers and sessile species can be complex and differ between taxonomic groups (Moore & Crawley 2014). Grazing may also prevent the spread of species to higher elevations as climate

warms and mediate the response of vegetation communities to climatic change: this may be particularly pronounced in low productivity, stress-tolerant communities. (Virtanen et al. 2010).

Analysis (ii): cross-scale productivity

As well as improved methods to process DEMs, data availability itself has opened new avenues. Remotely sensed data allow for continuous and consistent measurement of spatial and temporal phenomena, and the value of these data has been recognised in ecology for some time (Turner et al. 2003; Wang et al. 2010; Boyd 2009). However, these data are underused in geodiversity research to date. One of the most widely-used remote sensing-derived metrics in ecology is that of NDVI (Pettorelli et al. 2005; Pausas & Ribeiro 2017), which we used as our measure of productivity. It is widely considered to be reasonable measure of productivity in places where vegetation is not too dense (Šímová & Storch 2016).

In our study, elevation was consistently dominant in our models of mean and standard deviation in NDVI across several different grid sizes, suggesting that topography relates to both the overall and heterogeneity in productivity at our site. Mean productivity declined with increasing elevation, which runs contrary to a study in a contrasting environment (forest–alpine tundra ecotone) in northern Finland, which found that NDVI increased with increasing elevation, probably because of the greater light and radiation availability (Riihimäki et al. 2017). At our study site, the exposed higher ground generally precludes the formation of soils (Fig. 1ii), thus limiting productivity, despite resource levels relating to light and radiation. However, variation in productivity increased with elevation, meaning that productivity was more consistent within a given grid cell at lower levels. This most likely relates to the greater heterogeneity in the land surface at higher elevations (e.g. thin soils interspersed with bare ground because of the exposed environment and high winds).

Mean productivity declined further away from rivers because these lower, riverine environments are generally more sheltered against high winds, have lower mean and extreme temperatures, and have greater moisture levels that promote resource availability and therefore productivity (Wrightham & Kempe 2006). Hydrological and edaphic conditions therefore seem to constitute the dominant control on mean productivity rather than light and radiation (proxies for which are elevation and aspect: Riihimäki et al., 2017) in our relatively small river catchment. Of the non-hydrological geodiversity data, spur and ridge landforms identified areas that generally had a lower productivity across all scales, suggesting an additional relevant factor beyond elevation and hydrology. Such landforms are often exposed,

helping to explain the lower productivity in windier and colder environments, which often have a thinner or non-existent soil layer (Gordon et al. 2006; Vandvik et al. 2005). Deflation surfaces may be present on ridge features, for example (Wrightham & Kempe 2006). There was also a model interaction between these landforms and elevation. These results may be significant when we consider that greater changes are expected under climate change in more productive environments (Virtanen et al. 2010). Monitoring of this site's vegetation plots may be revealing in this regard in the future.

Data

The landform data used here were mapped using a relatively high resolution DEM (5 x 5 m) and geomorphometric techniques in GRASS GIS. The landform classification at this fine scale was relatively crude, however, compared to a professionally mapped landform dataset (either in the field or from fine-scale aerial photography). This situation with landform data therefore presents a trade-off between relatively cheap, consistent, semi-automated landform mapping and expensive professional surveys. Geodiversity data are considered to be cheaper than biodiversity data and techniques such as automatic landform mapping support this view further (Hjort et al. 2012). However, whilst the relatively crude landform data were clearly useful in this study, it would be informative to know whether specific information on smaller, more specific landforms was additionally useful. This remains an open question and no such comparison has been undertaken.

The superficial deposit map from the British Geological Survey (BGS) and the geomorphological classifications map from Scottish Natural Heritage (SNH; Table 1) were mapped at a 1:10,000 scale and at 12.5 x 12.5 m, respectively, whilst the soil parent material data were coarser (1:50,000). Finer-scale data on surface materials from field mapping might have proved useful and identified further links between species and geofeatures, but these data do not presently exist and would have required extensive field surveys. Remote sensing and unmanned aerial vehicle (UAV) technology may improve the prospects for low-cost geological and geomorphological mapping in the future, as well as for mapping landforms (Fernández-lozano & Gutierrez-alonso 2016).

For some species where we would have expected geofeature relationships, geofeatures explained zero or near-zero variance in the models, with traditional topographic measures having a model influence of over 95% for *Cladonia portentosa* (a lichen associated with peat bogs), *Carex bigelowii* (a sedge that is typically found in or near boggy areas), and *Dicranum majus* (a moss commonly found in ravines). For the last species it is also found on scree slopes

and in forests, which may explain difficulty in linking its distribution to a particular geofeature (RBGE, 2017). However, for the other two examples, these shortcomings of our models and failure to identify geofeatures that explained species' distributions may be attributable to collinearities between geofeatures and topography or simply to the fact that we did not include geofeature data at a fine enough scale for relationships to be detected. These were the extreme examples, but there were other species' distributions mostly explained by topography where we would have expected greater model influence from geofeatures.

Patterns of Life under future environmental change

Recent research in conservation biology has discussed the advantages of 'Conserving Nature's Stage' in a time of global environmental change (Anderson & Ferree 2010; Lawler et al. 2015). Indeed, geophysically diverse locations may be more resilient to climatic changes and facilitate species' capacity to adapt to climate change (Albano 2015). This may be especially relevant considering how a number of climate change mechanisms are projected to operate differentially across the world (Ordonez et al. 2016b) and that significant upward vegetation shifts have already been recorded (Lenoir et al. 2008). The authors here suggested that preserving geophysical settings could be the best strategy in places expected to experience intermediate disturbances from climate (also see Anderson & Ferree 2010). Meanwhile, species in areas facing immediate disturbance may require relocation or be lost.

In upland environments, biotic homogenisation has been recorded in recent decades (Ross et al. 2012) and the sensitivity of plant communities highlighted (Morrocco et al. 2016), supporting the need for a fuller appreciation of fine- and landscape-scale links between the geophysical environment and ecology. The distribution of certain landforms has the potential to change with climate and there may be indirect effects on biota through changes in the frequency of disturbance events, and pH and moisture in soils and underlying geology, for example (Brazier et al. 2012; Le Roux et al. 2013). Meanwhile, temporal changes in species' distributions, abundance and productivity have been linked to short-term climatic change and geomorphological disturbance in high latitude environments (Virtanen et al. 2010). A clear way forwards is to sufficiently develop our knowledge of the processes that link species and productivity to explicit geofeatures (landforms and land surface materials) so that we can move towards the creation of mechanistic models that will help with conservation planning.

Towards this effort of better understanding links between species and geodiversity and between overall productivity and geodiversity, we have found that a number of datasets on landforms and land surface materials have enhanced our understanding of patterns of life

in an upland river catchment in the Central Scottish Highlands. Of the geodiversity data, landform information obtained from geomorphometric methods was particularly useful and highlighted parts of the landscape that were important for certain species and for productivity (or lack thereof) once the coarser environmental threshold of elevation (relating to temperature and exposure) had been passed.

In line with other studies (e.g. Bailey et al. 2017), we would therefore encourage analyses within this theme in different places and at different scales, so that we may better understand geodiversity's links to biodiversity and other metrics of living nature. Temporal analyses (e.g. Virtanen et al. 2010) require excellent data on geofeature changes (e.g. disturbance vents), species' distributions, and community composition analyses. For biotic change, cruder productivity measures based on remotely sensed derived NDVI (and derived products – e.g. the MODIS NPP), or other remotely sensed indicators of the status of vegetation[4], have the potential to improve temporal analyses in the absence of long-term ecological monitoring data. Meanwhile, for geofeature changes relating to disturbance, field surveys supported by aerial imagery (from aeroplanes or UAVs) may be required. Here, topographic predictors dominated, but it is the relatively small additive effects of geodiversity that constitute the key progression in terms of highlighting the value of geodiversity in elucidating ecological patterns. We hope that this exploratory study will pave the way for fine-scale geodiversity studies in ecology to explicitly test the geographical ubiquity of the patterns found here in different places and also through time.

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[4] e.g. http://www.sentinel-hub.com/apps/wms/wms-parameters/EOproducts

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THESIS SUMMARY

Paper №	Title	Rationale, main aim, and key outcomes or findings
I	Geodiversity, Ecological Mechanisms, and Scale: Assessment and Prospect	**Rationale:** Geodiversity has not previously been fully incorporated into ecological theory because of its origins in geology and geomorphology. **Outcomes:** By viewing geodiversity through the eye of an ecologist, explicit theoretical links between geodiversity and ecology are established and summarised more extensively than ever before. Furthermore, a cross-scale spatio-temporal framework is developed, alongside a workflow for ecologists wishing to use geodiversity in research.
II	Modelling native and alien vascular plant species richness: at which scales is geodiversity most relevant?	**Rationale and aim:** The spatial scales at which geodiversity is relevant to species richness have never been investigated, and nor do we know whether it is more useful for modelling native or alien species. Therefore, vascular plant richness (native and alien) was modelled across multiple spatial scales (grains size and extent) across the whole of Great Britain. **Key finding:** Geodiversity improved our understanding of, and ability to model, the relationship between plant species richness and abiotic heterogeneity at multiple spatial scales, but especially the landscape scale and for native species.
III	Combining geodiversity with climate and topography to account for threatened species richness	**Rationale and aim:** There are important conservation and management issues surrounding threatened species, yet links between geodiversity, which has been hailed as a useful tool in conservation biology, and threatened species remain elusive. Therefore, geodiversity-threatened species relationships were studied across all of Finland's national parks. **Key finding:** Higher levels of geodiversity were consistently associated with increased threatened species richness across taxa; the combined effect of geodiversity variables was greater still in the rarity-weighted richness (RWR) analyses (except for fungi).
IV	Modelling common and rare plant diversity and distributions in relation to geodiversity in an upland landscape	**Rationale and aim:** Despite an increasing, albeit still limited, body of work on geodiversity–species richness relationships, we severely lack knowledge on how individual species' distributions relate to geodiversity and geofeatures, including in mountainous landscapes where geodiversity is thought to be most relevant. This study therefore assessed patterns of rare and common plant species in a sensitive upland environment (the Cairngorms, Scotland). **Key finding:** The inclusion of novel geodiversity data, and its constituent geofeatures, revealed previously unknown links between species and the geophysical environment at this macroecological scale.
V	Relating geodiversity to species' distributions and cross-scale productivity in an upland river catchment	**Rationale:** Much work remains to be done on identifying the spatial scales at which geodiversity is most applicable to biodiversity; links between geodiversity and productivity are virtually unstudied. However, a fuller understanding of these cross-scale relationships should be able to inform conservation efforts. **Key finding:** We successfully linked plot-scale species' distributions and overall productivity (measured by NDVI) to specific geofeatures and, for the former, these links were often understandable in line with species' known ecology.

Outstanding Questions

As outlined at the end of PAPER I, there are a number of clear pathways to follow as we move forwards with geodiversity research. The key questions are:

1. Where is geodiversity most relevant taxonomically and geographically, and at what spatio-temporal scales across taxa and geographic space, for advancing our understanding of patterns of life? Anthropogenic, marine, and freshwater environments should be considered, in addition to the terrestrial ones considered here.
2. Which facets of 'patterns of life' correspond most closely to different measures of geodiversity? These might include, but are not limited to: species richness; species' distributions; beta diversity; rarity-weighted richness (RWR). Comparable geodiversity metrics, based on explicit geofeatures, should be developed.
3. Where does the role of environmental heterogeneity (including geodiversity) peak in improving biodiversity models? Are extremely heterogeneous locations less diverse than those with intermediate heterogeneity?
4. To what extent can geodiversity and geofeatures inform our understanding of patterns in species' traits across spatial scales?
5. Can geodiversity help explain holes in species distributions?
6. Exactly how can geofeatures and geodiversity be used to improve ecological forecasting under climate change? This may extend to refugia.
7. Are automatically and semi-automatically derived geofeature data from digital elevation models (DEMs) better than expertly-mapped data in terms of how much they enhance our ecological modelling and how much they cost to produce (time and money)?

Conclusion

Prior to the works presented in this thesis, studies linking environmental heterogeneity to patterns of life typically involved crude parameters, such as standard deviation of elevation and slope, derived from digital elevation models. The value of these metrics has in fact been corroborated here. However, environmental heterogeneity research has been advanced by utilising geomorphometric techniques to quantify explicit geofeatures within the landscape, for which I have outlined the theoretical links to ecology using existing principles and theories. These data were combined with geological and hydrological data to assess patterns of life in relation to geodiversity, which allows us to identify a wider range of landscape properties that define true environmental heterogeneity and affect patterns of life through abiotic conditions and their effects on ecological processes.

Reflecting upon the quotation by Murray Gray (p. iii) and the need for a "holistic approach" to nature "that includes both geodiversity and biodiversity", the works within this thesis entirely support this outlook, empirically and conceptually. Indeed, the living and non-living natural worlds are intimately connected and geodiversity allows for us to make these connections in a logical and realistic way, such that it represents a clear progression in how we measure and conceptually approach abiotic nature.

Entrenching a holistic interpretation of nature in science, policy and conservation may be more attainable by using geodiversity, hopefully to the advantage of the living, abiotic and human domains that occupy the landscapes of planet Earth, now and in the future.

SUPPORTING

INFORMATION

PAPER II: SUPPORTING INFORMATION

Paper title: Modelling native and alien vascular plant species richness: at which scales is geodiversity most relevant?

Paper II SI: Summary

All SI, including purely digital material not provided below**, can be accessed via:

- https://www.dropbox.com/s/r81j86asojcyt3q/JJB_2017_PhD_SI.zip
  (password: cGZdzP6Ze8)
- Or, the paper's Wiley page: http://onlinelibrary.wiley.com/doi/10.1111/geb.12574/full

Appendix S1: Details of data sources in Table 1

Appendix S2: Geomorphometry Details

*Appendix S3 (caption): Climate, topography, geodiversity, and geofeature maps***

Appendix S4: Details of BRT modelling simplification

*Appendix S5 (caption): High resolution version of Fig. 3***

*Appendix S6 (caption): Full version of Fig. 4***

Appendix S7: Model interactions summary

*Appendix S8 (caption): Collinearity summary across scales***

Appendix S9a: Correlation matrix, national extent, fine (1 km2) grain

Appendix S9b: Correlation matrix, national extent, coarse (10 km2) grain

*Appendix S10 (caption): Full version of Fig. 5 (model fit statistics; self-statistics)***

*Appendix S11 (caption): Model evaluation statistics (CV)***

Appendix S12: Remote sensing of GDCs

Paper II SI: Appendix S1

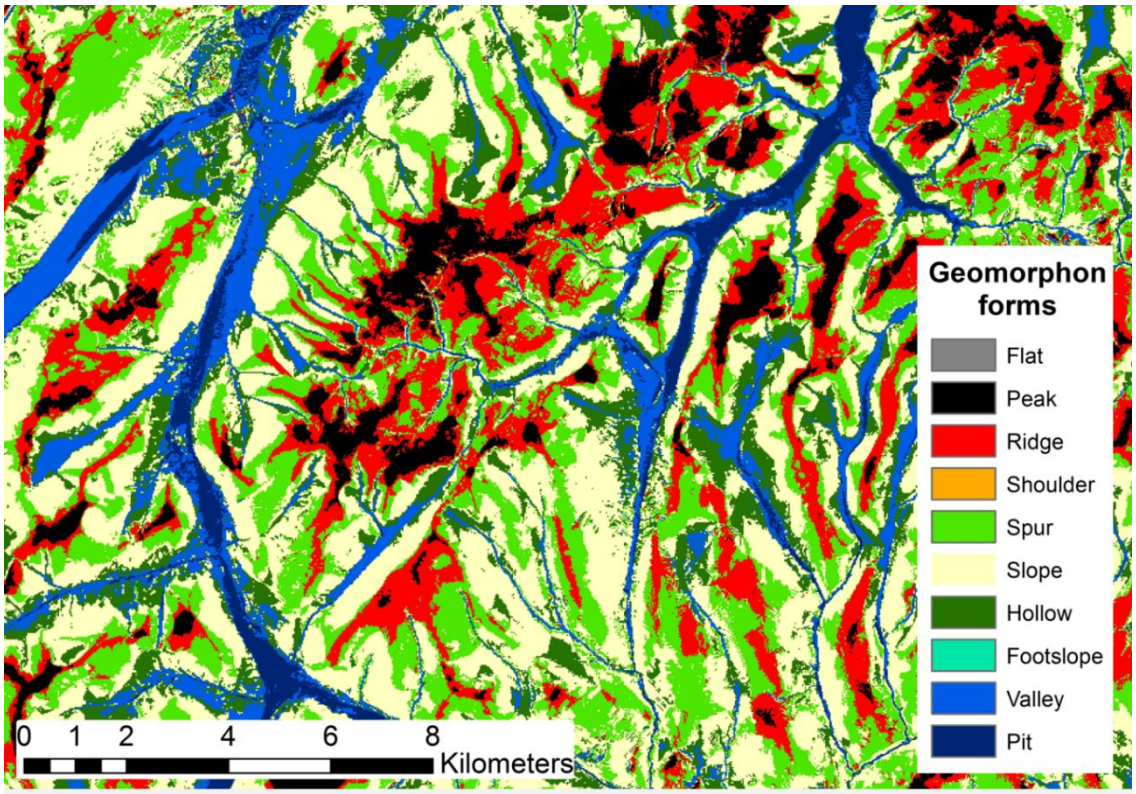
Details of data sources referenced in **Table 1** and in the methods. *All URLs were last checked on September 7th, 2016

Reference	Organisation / database / manual	URL(s)	License / comments
BGS (2015)	British Geological Survey	http://www.bgs.ac.uk/data/services/digmap50wms.html	Licence No. 2014/128 ED British Geological Survey © NERC. All rights reserved
BSBI (2015)	Botanical Society of Britain and Ireland Distribution Database.	http://bsbidb.org.uk/	Also see Walker et al. (2010) for information on sampling and see **Acknowledgements**.
Casweb (2015)	Access to UK census aggregate data	http://casweb.mimas.ac.uk/*	Comment: Casweb is part of the UK Data Service Census Support CP
CLC (2013)	Corine Land Cover 2006 raster data: Version 17 (12/2013) - Raster data on land cover for the CLC2006 inventory	http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3	Comment: The 100m resolution data were used in this study.
Hijmans et al. (2005)	Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965–1968.	http://www.worldclim.org/ & http://onlinelibrary.wiley.com/doi/10.1002/joc.1276/pdf	NA
NEODC (2015); NERC (2015); Intermap (2015)	**NERC's** Earth Observation Data Centre (**NEODC**) was used to download **Intermap's** NEXTMap DEM	http://neodc.nerc.ac.uk/ & http://www.intermap.com/	End User License Agreement (EULA) for NEXTMap Britain dataset, v1.0 25/10/2004 MJP confirmed on the 19th May 2014.
OS Strategi (2015); Edina Digimap (2015).	Ordnance Survey Strategi: free vector map datasets via **Edina Digimap** under Open License.	https://www.ordnancesurvey.co.uk/business-and-government/products/strategi.html	Open UK Government License (see http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/).

Paper II SI: Appendix S2

Details on automated landform extraction (geomorphometry).

An `r.geomorphon` (Jasiewicz and Stepinski, 2013) output over part of central Scotland is shown. Produced in GRASS GIS 7.1. These geomorphon data were produced nationally and the coverage (%) of each landform type summarised for each 1km^2 and 100km^2 grid cell.



Online resources to support use of this algorithm in GRASS GIS 7:

- Jasiewicz and Stepinski (2013): http://www.sciencedirect.com/science/article/pii/S0169555X12005028
- GRASS GIS r.geomorphon manual: https://grass.osgeo.org/grass70/manuals/addons/r.geomorphon.html

Expansion on methodological details and validation, and some issues to be tackled

After experimentation to balance accuracy with computation time, the algorithm used a search radius of 2km. This meant that very large features (e.g. long valleys and ridges) were successfully extracted, whilst small features (e.g. hollows and peaks) were mapped as they would have been under a smaller search radius. Data were qualitatively assessed for accuracy using Google Earth, ArcScene (by visualising landform coverage data atop a 3D DEM), and our

personal knowledge of landscape features across Great Britain and within specific parts of it; we have a very high confidence in the data produced.

We used the 25 meter DEM. Computation time for finer DEMs was increased substantially and, as discovered from tests in parts of Great Britain, a finer grain size did not necessarily improve landform identification. Indeed, at times, the results simply became noisy and landform features were missed. The relationship between the DEM cell size and the accuracy of this algorithm presents an interesting question that we wish to see explored. For example, if one had higher resolution DEM data, for example that provided by airborne LiDAR with a high point density, would this be a useful algorithm? Or would the data simply be too fine and noisy for it to identify landforms in a useful way? We welcome analyses and discussion around such questions.

Paper II SI: Appendix S3 (caption)

Climate, topography, geodiversity, and geofeature maps.

Stored as a separate PDF: 'Bailey_et_al_SI_Appendix_S3_maps_slideshow.pdf'.

A slideshow of selected maps of Great Britain's climate, topography, geodiversity, and geofeatures aggregated to the coarser grain size of 10x10 km (hectad).

Paper II SI: Appendix S4

Details of BRT modelling simplification.

In each case, an initial model was produced for whichever predictor set was being used (geodiversity information only, no geodiversity information, or all variables). Predictors were then removed if their model contribution (i.e. relative influence on the model) was < 10%. This was occasionally reduced to < 7.5% in rare cases where removing predictors with <10% resulted in too few predictors to run the second model. This new predictor set of the most highly contributing variables was then used to create a simplified model where predictors could contribute <10%. This approach was chosen over using '`gbm.simplify`', an integrated simplification function in the `gbm` package, because it allowed for greater flexibility to match our requirements. The results presented are always for the simplified models when they were available.

Paper II SI: Appendix S5 (caption)

High resolution version of Fig. 3

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'Bailey_et_al_SI_Appendix_S5_boxplots_High_Res_Fig_3.jpg'

Figure caption: Combined model contributions (%) of each predictor set (climate, topography, geodiversity) and geodiversity subset, as well as isolated predictors human population and land cover variety. All scales are shown: grain sizes (1x1km cells in blue, 10x10km in green) and extent diameters (lighter [further left] = smaller). This plot shows only model contributions of each predictor set, and gives no indication of directionality. 'Pop' = population.

Paper II SI: Appendix S6 (caption)

Full version of Fig. 4

Stored as a separate image file:
'Bailey_et_al_SI_Appendix_S6_boxplots_GDCs_Full_Fig_4.jpg'.

Figure caption: Model contributions from individual GDCs at the 1x1km grain size for each extent. These graphs are truncated at +50% and -50%, but only a small minority of points lie beyond these values. 'Sup. Dep.' = superficial deposits.

Paper II SI: Appendix S7

Model interactions summary. A qualitative summary of the most frequent dominant model interactions amongst model inputs (↔). More frequent interactions are at the top of each scale's results. 'Clim' (climate) and 'Topo' (topography)' are often used to refer to an unspecified mixture of variables from these predictor sets. '&' denotes separate interactions: e.g. "Pop ↔ Mean Elev & River Length" = "Pop ↔ Mean Elev & Pop ↔ River Length". 'Pop' = human population; 'Elev' = elevation; 'Temp' = annual mean temperature; 'Prec' = annual precipitation; 'LCV' = land cover variety; 'Geo' = geological; 'SD' = standard deviation.

Grain size	Extent radius	Species group				
		All	**Native**	**Alien**	**Arch.**	**Neophyte**
1x1 km	**12.5km**	Clim ↔ SD Slope & Clim & Mean Elev	Clim ↔ Clim & Mean Elev Mean Elev ↔ SD Slope	Pop ↔ Mean Elev & Clim Clim ↔ Clim & Mean Elev	Clim ↔ Clim & Mean Elev Prec ↔ Hollows & Slopes	Pop ↔ Mean Elev & Clim & SD slope & River Length
	25km	Clim ↔ Clim & SD Slope Mean Elev ↔ SD Slope	Clim ↔ Clim & SD Slope	Clim ↔ Clim & Mean Elev Mean Elev ↔ SD Slope	Clim ↔ Clim & Mean Elev& Pop Pop ↔ Mean Elev & Clim	Pop ↔ Mean Elev & Clim & SD slope & River length & Hollows
	50km	Clim ↔ Clim & SD Slope Mean Elev ↔ SD Slope	Clim ↔ Clim & SD Slope	Clim ↔ Clim & Mean Elev	Pop ↔ Mean Elev & Clim	Pop ↔ Clim & Mean Elev & SD Slope
	75km	Clim ↔ Clim & SD Slope & Mean Elev	Clim ↔ Clim & Mean Elev	Clim ↔ Mean Elev & Pop Mean Elev ↔ Pop	Clim ↔ Clim & Mean Elev & Pop	Pop ↔ Clim & Mean Elev & SD Slope Clim ↔ Clim
	100km	Clim ↔ Clim & Pop & SD Slope	Clim ↔ Clim & Mean Elev	Clim ↔ Mean Elev & Pop	Clim ↔ Clim & Mean Elev & Pop Pop ↔ Spurs	Pop ↔ Clim & SD Slope Clim ↔ Clim
	125km	Clim ↔ Clim & Pop	Clim ↔ Clim & SD Slope	Clim ↔ Mean Elev & Pop	Clim ↔ Clim & Mean Elev & Pop Pop ↔ Spurs	Pop ↔ Clim & SD Slope Clim ↔ Clim
	National	Clim ↔ Clim	Clim ↔ Clim	Clim ↔ Clim & Pop Pop ↔ Prec	Clim ↔ Clim & River Length	Clim ↔ Clim & Pop Pop ↔ Prec
10x10 km	**50km**	Clim ↔ Clim & Pop & River Length	Clim ↔ Clim & Pop & LCV & Geo variety	Clim ↔ Clim & Pop Pop ↔ River Length & Mean Elev		
	75km	Clim ↔ Clim & Pop	Clim ↔ Clim & Pop & LCV	Clim ↔ Clim & Pop Pop ↔ Mean Elev		
	100km	Clim ↔ Clim & Pop	Clim ↔ Clim & Pop & River Length	Clim ↔ Clim & Pop		
	125km	Clim ↔ Clim & Pop	Clim ↔ Clim & Pop & River Length	Clim ↔ Clim & Pop		
	National	Clim ↔ Clim & Pop & LCV Pop ↔ Temp	Temp ↔ LCV Clim ↔ Clim & Pop	Pop ↔ Temp Clim ↔ Clim & Pop	Clim ↔ Clim & Pop & River Length	Pop ↔ Temp Clim ↔ Clim & Pop

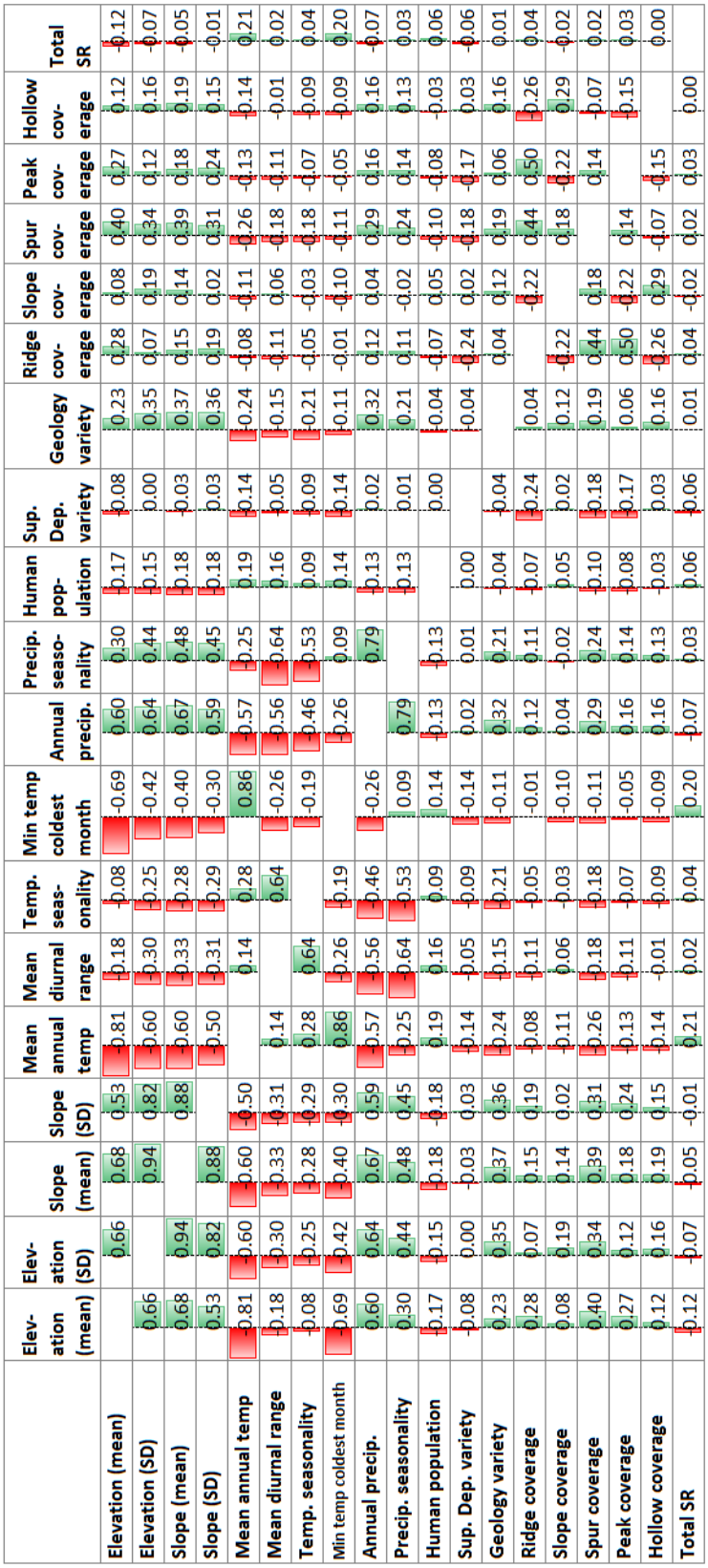
Paper II SI: Appendix S8 (caption)

Stored as a separate image file: 'Bailey_et_al_SI_Appendix_S8_collinearities.jpg'.

Figure caption: An overview of all correlations between all abiotic predictors (not species richness). All sub-national scales are shown (see **Appendix S9** for national): grain sizes (1x1km cells in blue, 10x10km in green) and extent diameters (lighter [further left] = smaller). A correlation matrix was produced for each region and scale (e.g. 25 km extent, 1 km^2 grain size, around a given grid cell centroid). All of the values have then be summarised here with a graph per predictor to show the range of correlations between the focal predictor and all other abiotic predictors. **Bioclimatic variables (WorldClim):** 1 (Annual Mean Temperature), 2 (Mean Diurnal Range (Mean of monthly (max temp - min temp))), 4 (Temperature Seasonality (standard deviation *100)), 6 (Min Temperature of Coldest Month), 12 (Annual Precipitation), 15 (Precipitation Seasonality (Coefficient of Variation)).

Paper II SI: Appendix S9a

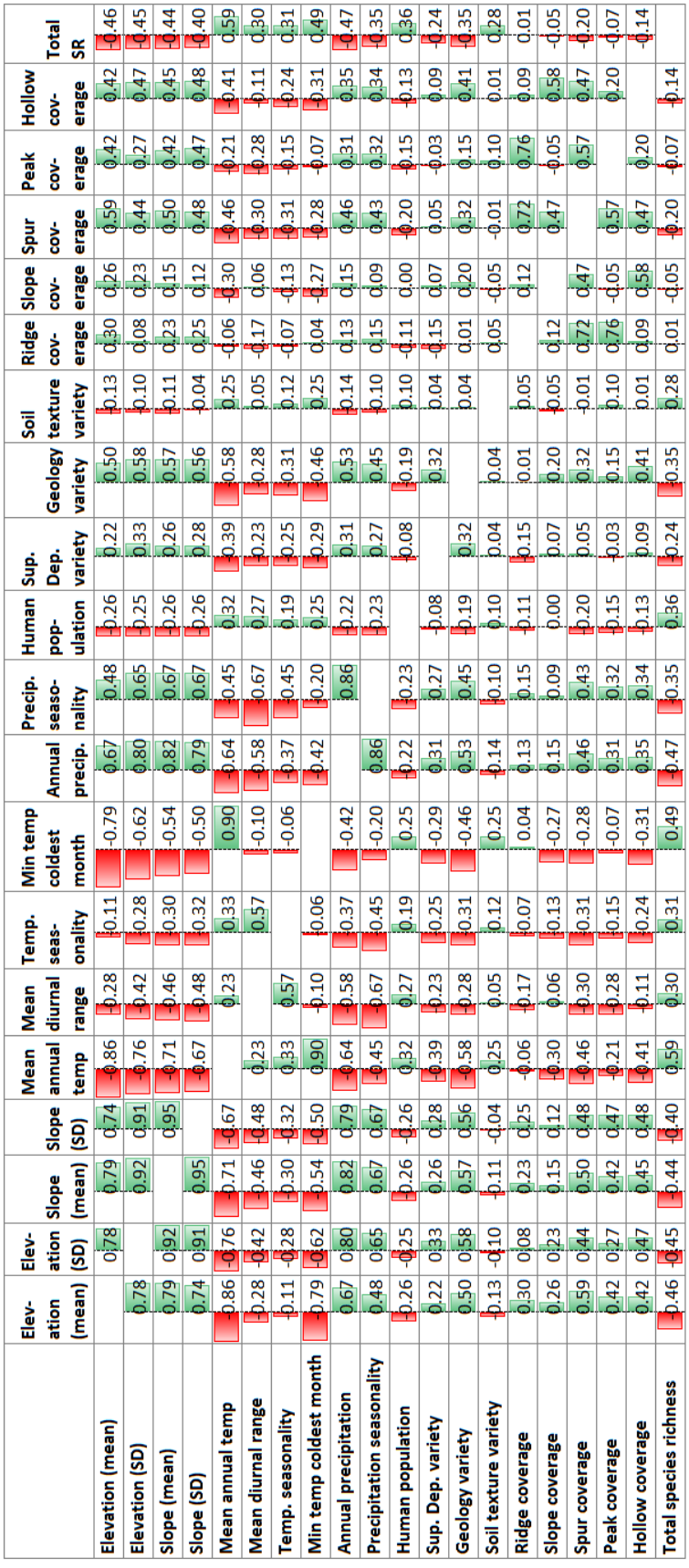
Correlation matrix, national extent, fine (1 km²) grain



	Elev-ation (mean)	Elev-ation (SD)	Slope (mean)	Slope (SD)	Mean annual temp	Mean diurnal range	Temp. seas-onality	Min temp coldest month	Annual precip.	Precip. seaso-nality	Human pop-ulation	Sup. Dep. variety	Geology variety	Ridge cov-erage	Slope cov-erage	Spur cov-erage	Peak cov-erage	Hollow cov-erage	Total SR
Elevation (mean)		0.66	0.68	0.53	-0.81	0.18	-0.08	-0.69	0.60	0.30	0.17	0.08	0.23	0.28	0.08	0.40	0.27	0.12	0.12
Elevation (SD)	0.66		0.94	0.82	-0.60	0.30	-0.25	-0.42	0.64	0.44	0.15	0.00	0.35	0.07	0.19	0.34	0.12	0.16	0.07
Slope (mean)	0.68	0.94		0.88	-0.60	0.33	-0.28	-0.40	0.67	0.48	0.18	0.03	0.37	0.15	0.14	0.39	0.18	0.19	0.05
Slope (SD)	0.53	0.82	0.88		-0.50	0.31	-0.29	-0.30	0.59	0.45	0.18	0.03	0.36	0.19	0.02	0.31	0.24	0.15	0.01
Mean annual temp	-0.81	-0.60	-0.60	-0.50		-0.14	0.28	0.86	-0.57	-0.25	-0.19	-0.14	-0.24	-0.08	-0.11	-0.26	-0.13	-0.14	-0.21
Mean diurnal range	0.18	0.30	0.33	0.31	-0.14		0.64	-0.26	-0.56	-0.64	-0.16	-0.05	-0.15	-0.11	-0.06	-0.18	-0.11	-0.01	-0.02
Temp. seasonality	-0.08	-0.25	-0.28	-0.29	0.28	-0.64		-0.19	-0.46	-0.53	-0.09	-0.09	-0.21	-0.05	-0.03	-0.18	-0.07	-0.09	-0.04
Min temp coldest month	-0.69	-0.42	-0.40	-0.30	0.86	-0.26	-0.19		-0.26	-0.13	-0.14	-0.14	-0.11	-0.01	-0.10	-0.11	-0.05	-0.09	-0.20
Annual precip.	0.60	0.64	0.67	0.59	-0.57	0.56	-0.46	-0.26		0.79	0.13	0.02	0.32	0.12	0.04	0.29	0.16	0.16	0.07
Precip. seasonality	0.30	0.44	0.48	0.45	-0.25	0.64	-0.53	-0.09	0.79		0.13	0.01	0.21	0.11	0.02	0.24	0.14	0.13	0.03
Human population	0.17	0.15	0.18	0.18	-0.19	0.16	0.09	0.14	0.13	0.13		0.00	0.04	0.07	0.10	0.19	0.08	0.03	0.06
Sup. Dep. variety	0.08	0.00	0.03	0.03	-0.14	0.05	0.09	0.14	0.02	0.01	0.00		0.04	0.24	0.02	0.18	0.17	0.03	0.06
Geology variety	0.23	0.35	0.37	0.36	-0.24	0.15	0.21	0.11	0.32	0.21	0.04	0.04		0.04	0.12	0.19	0.16	0.01	0.06
Ridge coverage	0.28	0.07	0.15	0.19	-0.08	0.11	0.05	0.01	0.12	0.11	0.07	0.24	0.04		0.22	0.44	0.50	0.26	0.04
Slope coverage	0.08	0.19	0.14	0.02	-0.11	0.06	0.03	0.09	0.16	0.13	0.03	0.03	0.16	0.26	0.29	0.07	0.15	0.00	0.00
Spur coverage	0.40	0.34	0.39	0.31	-0.26	0.18	0.18	0.11	0.29	0.24	0.10	0.18	0.19	0.44	0.18	0.14	0.07	0.02	0.02
Peak coverage	0.27	0.12	0.18	0.24	-0.13	0.11	0.07	0.05	0.16	0.14	0.08	0.17	0.06	0.50	0.22	0.14	0.15	0.03	0.03
Hollow coverage	0.12	0.16	0.19	0.15	-0.14	0.01	0.09	0.09	0.16	0.13	0.03	0.03	0.16	0.26	0.29	0.07	0.15	0.00	0.00
Total SR	0.12	0.07	0.05	0.01	-0.21	0.02	0.04	0.20	0.07	0.03	0.06	0.06	0.01	0.04	0.02	0.02	0.03	0.00	

Paper II SI: Appendix S9b

Correlation matrix, national extent, coarse (10 km²) grain



	Elev-ation (mean)	Elev-ation (SD)	Slope (mean)	Slope (SD)	Mean annual temp	Mean diurnal range	Temp. seas-onality	Min temp coldest month	Annual precip.	Precip. seaso-nality	Human pop-ulation	Sup. Dep. variety	Geology variety	Soil texture variety	Ridge cov-erage	Slope cov-erage	Spur cov-erage	Peak cov-erage	Hollow cov-erage	Total SR
Elevation (mean)		0.78	0.79	0.74	-0.86	-0.28	0.11	-0.79	0.67	0.48	-0.26	0.22	0.50	0.13	0.30	0.26	0.59	0.42	0.42	-0.46
Elevation (SD)	0.78		0.92	0.91	-0.76	-0.42	0.28	-0.62	0.80	0.65	-0.25	0.33	0.58	0.10	0.08	0.23	0.44	0.27	0.47	-0.45
Slope (mean)	0.79	0.92		0.95	-0.71	-0.46	0.30	-0.54	0.82	0.67	-0.26	0.26	0.57	0.11	0.23	0.15	0.50	0.42	0.45	-0.44
Slope (SD)	0.74	0.91	0.95		-0.67	-0.48	0.32	-0.50	0.79	0.67	-0.26	0.28	0.56	0.04	0.25	0.12	0.48	0.47	0.48	-0.40
Mean annual temp	-0.86	-0.76	-0.71	-0.67		0.23	0.33	0.90	-0.64	-0.45	0.32	-0.39	0.58	0.25	-0.06	-0.30	-0.46	-0.21	-0.41	0.59
Mean diurnal range	-0.28	-0.42	-0.46	-0.48	0.23		0.57	-0.10	-0.58	-0.67	0.27	-0.23	0.28	0.05	-0.17	-0.06	-0.30	-0.28	-0.11	0.30
Temp. seasonality	-0.11	-0.28	-0.30	-0.32	0.33	0.57		-0.06	-0.37	-0.45	0.19	-0.25	0.31	0.12	-0.07	-0.13	-0.31	-0.15	-0.24	0.31
Min temp coldest month	-0.79	-0.62	-0.54	-0.50	0.90	0.23	0.06		-0.42	-0.20	0.25	-0.29	0.46	0.25	0.04	-0.27	-0.28	-0.07	-0.31	0.49
Annual precipitation	0.67	0.80	0.82	0.79	-0.64	-0.58	0.37	-0.42		0.86	-0.22	0.31	0.53	0.14	0.13	0.15	0.46	0.31	0.35	-0.47
Precipitation seasonality	0.48	0.65	0.67	0.67	-0.45	-0.67	0.45	-0.20	0.86		-0.23	0.27	0.45	0.10	0.15	0.09	0.43	0.32	0.34	-0.35
Human population	-0.26	-0.25	-0.26	-0.26	0.32	0.23	0.19	0.25	-0.22	-0.23		-0.08	0.19	0.10	0.11	0.00	0.20	0.15	0.13	-0.36
Sup. Dep. variety	0.22	0.33	0.26	0.28	-0.39	-0.23	0.25	-0.29	0.31	0.27	-0.08		0.32	0.04	0.15	0.07	0.05	0.07	0.09	-0.24
Geology variety	0.50	0.58	0.57	0.56	-0.58	-0.28	0.31	-0.46	0.53	0.45	-0.19	0.32		0.04	0.01	0.20	0.32	0.15	0.41	-0.35
Soil texture variety	0.13	0.10	0.11	0.04	-0.25	-0.05	0.12	-0.25	0.14	0.10	-0.10	0.04	0.04		0.05	0.01	-0.01	0.10	0.01	-0.28
Ridge coverage	0.30	0.08	0.23	0.25	-0.06	-0.17	0.07	-0.04	0.13	0.09	-0.00	-0.15	0.01	0.05		0.12	0.72	0.76	0.09	-0.01
Slope coverage	0.26	0.23	0.15	0.12	-0.30	-0.06	0.13	-0.27	0.15	0.09	-0.11	-0.07	0.20	0.05	0.12		0.47	0.05	0.58	-0.05
Spur coverage	0.59	0.44	0.50	0.48	-0.46	-0.30	0.31	-0.28	0.46	0.43	-0.20	0.05	0.32	0.01	0.72	0.47		0.57	0.47	-0.20
Peak coverage	0.42	0.27	0.42	0.47	-0.21	-0.28	0.15	-0.07	0.31	0.32	-0.15	-0.03	0.15	0.10	0.76	0.05	0.57		0.20	-0.07
Hollow coverage	0.42	0.47	0.45	0.48	-0.41	-0.11	0.24	-0.31	0.35	0.34	-0.13	0.09	0.41	0.01	0.09	0.58	0.47	0.20		-0.14
Total species richness	-0.46	-0.45	-0.44	-0.40	0.59	0.30	0.31	0.49	-0.47	-0.35	0.36	-0.24	0.35	0.28	0.01	-0.05	0.20	0.07	0.14	

Paper II SI: Appendix S10 (caption)

Stored as a separate image file: 'Bailey_et_al_SI_Appendix_S10_fit_stats_Full_Fig_5.jpg'.

Figure caption: A full version of Fig. 5. Comparison of model fit statistics (self-statistics; SS) with and without geodiversity according to grain size (colour/shade) and extent (x-axis).* = significant ($p < 0.01$, paired t-test) average model improvement across all models when comparing those without geodiversity (the middle boxplot for each scale) to those with all predictors (the right boxplot). Values are given in Table 2.

Paper II SI: Appendix S11 (caption)

Stored as a separate image file: 'Bailey_et_al_SI_Appendix_S11_model_CV_eval_stats.jpg'.

Figure caption: As for S10, except mean cross-validation (CV) model evaluation statistics instead of internal fit 'self-statistics'.

Paper II SI: Appendix S12

Remote sensing of GDCs

A non-exhaustive summary of fine-scale geodiversity components (GDCs), within broad categories, which may be extracted via remote sensing techniques and used for biodiversity modelling (structure of categories derived from Hjort & Luoto, 2010). * = where exposed.

GM = geomorphology; GDC = geodiversity component; LSP = land surface parameter.

A full list of this table's references is given below the table.

Geo-feature	GDC	Dataset (in order of priority)	Example method of feature extraction (*Fusion of all data where possible*)	Ancillary data sources (Focussed on Great Britain)	Supporting literature (not exhaustive)
Geology	Coverage of surface/soil type (e.g. peat, till, sand, gravel)	Hyperspectral Lidar Photography/ High resolution	Per-pixel classification of spectral response/image texture. Supervised classification of Intensity/Full Waveform metrics. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BGS 1:50000 Geological map	McMorrow et al. (2004); Anderson and Croft (2009); Bretar et al. (2009); Hjort and Luoto (2010); Mulder et al. (2011); Bishop et al. (2012); Dutta et al. (2015).
Geology	Boulder	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation/structure from motion.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012). Hjort and Luoto (2010); Eltner et al. (2016).

GM – bedrock	Escarpment	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation/structure from motion.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012). Eltner et al. (2016).
GM – bedrock	Tor	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation/structure from motion.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Eltner et al. (2016).
GM – bedrock	Rocky outcrop	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation/structure from motion.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Eltner et al. (2016).
GM – bedrock	Fracture valley	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation/structure from motion.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Eltner et al. (2016).

GM – glacial	Corrie	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Negi et al. (2015).
GM – glacial	Moraine (various)	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Negi et al. (2015).
GM – glacial	Kettle hole	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Rahmatulla et al (2012).
GM – glacial	Glaciofluvial channels	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012).

GM – glacial	Esker	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Negi et al. (2015).
GM – glacial	Kame	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Negi et al. (2015).
GM – glacial	Roches moutonnées	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR BRITICE dataset	Clark et al. (2004); Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Negi et al. (2015).
GM – fluvial	Gully	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Hopkins and Snyder (2016).

GM – fluvial	Oxbow Lake	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012).
GM – fluvial	Sandbar	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Wang et al. (2016).
GM – fluvial	River terrace	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Hopkins and Snyder (2016).
GM – Slope	Standard slope metrics	Lidar	Direct calculation of LSP from high resolution DTM – maximum rate of change in value from a cell to its direct neighbours in a 3x3 window.		Burrough and McDonnell (1998); Hengl and Router (2008).
GM – Slope	Debris flow	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012); Ninfo et al. (2016).

GM – Slope	Solifluction features	Lidar Hyperspectral* Photography*	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012).
GM – biogenic	Mire/ peat area	Hyperspectral Lidar Photography/ High resolution	Per-pixel classification of spectral response/image texture. Per-pixel classification of Intensity/Full Waveform metrics. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anderson et al. (2010); Anderson and Croft (2009); Bishop et al. (2012); Bretar et al. (2009).
Hydrology	Lake/ pond	Lidar Hyperspectral Photography/ High resolution	Production of LSPs from high resolution DTM used in object-based classification. Object-based classification of spectral response/image texture. Supporting visual interpretation.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Anders et al. (2011); Bishop et al. (2012); Evans (2012).
Hydrology	River/ stream	Lidar Hyperspectral Photography/ High resolution	Flow accumulation modelling using high resolution DTM. TWI measures may also be helpful as a hydrology proxy.	BGS 25cm RGB ortho aerial photography/50 cm CIR	Hjort and Luoto (2010); Evans (2012); Hengl and Router (2008); Hengle and Macmillan (2010); Marcus and Fonstad (2010); Pirotti and Tarolli (2010); Carbonneau and Piégay (2012).

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PAPER III: SUPPORTING INFORMATION

Paper title: Conserving Nature's stage? Combining geodiversity with climate and topography to account for threatened species diversity and rarity-weighted richness in Finland

Paper III SI: Summary

All SI (provided below) can also be accessed via

- https://www.dropbox.com/s/r81j86asojcyt3q/JJB_2017_PhD_SI.zip
  (password: cGZdzP6Ze8)
- Or, the paper's Wiley page: http://onlinelibrary.wiley.com/doi/10.1111/cobi.12799/full

Appendix S1: Information on the taxonomic groups included in the study

Appendix S2: Species list

Appendix S3: Species distribution modelling analyses

Appendix S4: Details of the modelling procedure of geomorphological richness

Paper III SI: Appendix S1

Taxonomic groups included in the study, their attributes and species with the most presence grid cells of each group. Taxonomic groups that are examined separately in diversity and/or distribution analysis are indicated with bold font.

Taxonomic group English name	Scientific name	Abbreviation	Number of 1-km study grid cells that include species	Number of species	Species with the most presence grid cells (and the number of those)
Fungi	***Fungi***	**FG**	**254**	**69**	***Antrodia albobrunnea* (110)**
Vascular plants	***Tracheophyta***	**VA**	**131**	**44**	***Calypso bulbosa* (27)**
Bryophytes	***Bryophyta***	**BR**	**54**	**53**	***Neckera pennata* (10)**
Lichens	***Lichenes***	**LI**	**39**	**44**	***Leptogium saturninum, Lobaria pulmonaria* (17)**
Beetles	***Coleoptera***	**CO**	**33**	**28**	***Pytho kolwensis, Quedius microps* (6)**
Butterflies and moths	***Lepidoptera***	**LE**	**18**	**13**	***Clepsis lindebergi, Ethmia quadrillella* (3)**
Mammals	***Mammalia***	**MA**	**17**	**2**	***Pteromys volans* (16)**
Molluscs	***Mollusca***	**MO**	**11**	**3**	***Macrogastra plicatula* (6)**
Two-winged flies	*Diptera*	DI	7	1	*Xylomya czekanovskii* (7)
True bugs	*Heteroptera*	HE	5	2	*Ceratocombus corticalis* (3)
Birds	*Aves*	AV	4	2	*Gavia stellata* (3)
Sawflies, wasps, bees and ants	*Hymenoptera*	HY	3	5	*Nomada moeschleri* (2)
Caddisflies	*Trichoptera*	TP	3	2	*Crunoecia irrorata* (2)
Stoneflies	*Plecoptera*	PP	2	1	*Nemoura dubitans* (2)
Amphibians	*Amphibia*	AM	1	1	*Triturus cristatus* (1)
Spiders	*Arenae*	AR	1	1	*Araneus angulatus* (1)
All species combined		**ALL**	**583**	**271**	***Antrodia albobrunnea* (110)**

Paper III SI: Appendix S2

The taxonomic groups and species included in the data, their International Union for the Conservation of Nature and Natural Resources (IUCN) classification (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, DD = Data Deficient) and the number of 1 km^2 study grid cells that include each species.

Taxonomic group	Species name	IUCN classification	Number of 1 km^2 grid cells including the species
Amphibia			1
	Triturus cristatus	EN	1
Arenae			1
	Araneus angulatus	NT	1
Aves			4
	Charadrius morinellus	NT	1
	Gavia stellata	NT	3
Bryophyte			54
	Anastrophyllum hellerianum	NT	6
	Anastrophyllum michauxii	VU	1
	Arnellia fennica	VU	3
	Athalamia hyalina	VU	1
	Bryum longisetum	EN	1
	Bryum pseudotriquetrum var. *neodamense*	VU	2
	Calypogeia suecica	VU	1
	Campyliadelphus elodes	VU	2
	Cephalozia macounii	CR	1
	Conocephalum salebrosum	VU	3
	Cyrtomnium hymenophylloides	NT	1
	Dicranum acutifolium	NT	1
	Geocalyx graveolens	NT	2
	Hamatocaulis vernicosus	VU	1
	Hypnum holmenii	NT	1
	Jungermannia confertissima	DD	1
	Jungermannia leiantha	NT	1
	Jungermannia obovata	NT	4
	Leiocolea badensis	VU	1
	Leiocolea bantriensis	NT	3
	Lophozia grandiretis	EN	1
	Lophozia longiflora	NT	2
	Moerckia hibernica	VU	2
	Myrinia pulvinata	NT	3
	Neckera pennata	VU	10
	Oncophorus elongatus	DD	1

	Oxystegus tenuirostris	NT	1
	Palustriella commutata	VU	1
	Palustriella decipiens	NT	1
	Palustriella falcata	NT	3
	Philonotis calcarea	EN	1
	Porella cordaeana	VU	1
	Pseudoleskeella rupestris	NT	1
	Riccardia palmata	NT	1
	Scapania aequiloba	EN	1
	Scapania apiculata	CR	1
	Scapania carinthiaca	CR	1
	Scapania cuspiduligera	VU	1
	Scapania gymnostomophila	NT	1
	Scapania paludosa	NT	1
	Scapania uliginosa	NT	1
	Schistidium sordidum	VU	1
	Schistostega pennata	NT	1
	Seligeria campylopoda	VU	1
	Seligeria diversifolia	NT	1
	Seligeria donniana	NT	1
	Seligeria tristichoides	VU	1
	Sphagnum inundatum	NT	1
	Timmia bavarica	VU	1
	Timmia comata	VU	2
	Trichocolea tomentella	VU	1
	Zygodon conoideus	EN	1
	Zygodon viridissimus	VU	2
Coleoptera			33
	Agathidium pulchellum	VU	3
	Agrilus ater	VU	2
	Anacaena globulus	VU	2
	Aulonothroscus laticollis	CR	2
	Boros schneideri	VU	4
	Carphacis striatus	NT	2
	Ceruchus chrysomelinus	EN	1
	Corticeus fraxini	NT	2
	Cyllodes ater	NT	2
	Epuraea silesiaca	NT	1
	Eucnemis capucina	NT	4
	Monochamus urussovii	NT	1
	Nothorhina punctata	NT	3
	Orthotomicus longicollis	VU	1
	Pedostrangalia pubescens	VU	2
	Pelecotoma fennica	NT	1
	Phytobaenus amabilis	NT	2
	Protaetia marmorata	VU	1

	Pytho abieticola	VU	2
	Pytho kolwensis	EN	6
	Quedius microps	NT	6
	Scraptia fuscula	NT	1
	Stephanopachys linearis	NT	3
	Stephanopachys substriatus	NT	2
	Trypophloeus asperatus	NT	1
	Trypophloeus discedens	NT	1
	Xyletinus tremulicola	VU	3
	Zavaljus brunneus	NT	1
Diptera			7
	Xylomya czekanovskii	VU	7
Fungi			254
	Amylocystis lapponica	NT	28
	Anomoloma albolutescens	VU	3
	Anomoloma myceliosum	NT	2
	Anomoporia bombycina	NT	4
	Antrodia albobrunnea	NT	110
	Antrodia crassa	EN	36
	Antrodia infirma	VU	59
	Antrodia mellita	NT	7
	Antrodia primaeva	VU	8
	Antrodia pulvinascens	VU	10
	Antrodiella canadensis	EN	2
	Antrodiella citrinella	NT	9
	Bovista paludosa	VU	1
	Ceriporia excelsa	NT	4
	Chlorencoelia versiformis	NT	6
	Cinereomyces lenis	NT	80
	Cortinarius odorifer	NT	2
	Crustoderma corneum	NT	24
	Crustoderma dryinum	NT	2
	Cystostereum murraii	NT	2
	Dentipellis fragilis	NT	1
	Dichomitus squalens	VU	4
	Diplomitoporus crustulinus	VU	1
	Diplomitoporus flavescens	NT	7
	Entoloma rubrobasis	NT	1
	Erastia salmonicolor	VU	1
	Fomitopsis rosea	NT	46
	Gelatoporia subvermispora	NT	2
	Gloeophyllum abietinum	NT	1
	Gloeophyllum protractum	VU	23
	Gloiodon strigosus	NT	11
	Haploporus odorus	NT	10
	Hebeloma syrjense	NT	1

	Hygrophorus gliocyclus	NT	1
	Laurilia sulcata	NT	12
	Lepiota audreae	NT	1
	Leucoscypha ovilloides	VU	1
	Marasmius siccus	NT	1
	Mycena tintinabulum	VU	1
	Odonticium romellii	NT	25
	Onnia tomentosa	NT	4
	Perenniporia subacida	NT	7
	Perenniporia tenuis	CR	1
	Phlebia centrifuga	NT	25
	Pholiota subochracea	NT	1
	Physisporinus rivulosus	VU	1
	Piloporia sajanensis	EN	1
	Postia guttulata	NT	10
	Postia lateritia	NT	24
	Postia parva	NT	11
	Protomerulius caryae	NT	26
	Pycnoporellus alboluteus	EN	3
	Radulodon erikssonii	VU	2
	Rigidoporus crocatus	EN	1
	Rugosomyces onychinus	NT	2
	Sarcodon leucopus	VU	2
	Sarcosphaera coronaria	EN	1
	Scytinostroma galactinum	NT	1
	Skeletocutis brevispora	NT	11
	Skeletocutis chrysella	NT	5
	Skeletocutis jelicii	EN	1
	Skeletocutis lilacina	VU	1
	Skeletocutis odora	NT	12
	Skeletocutis stellae	VU	20
	Steccherinum collabens	NT	8
	Steccherinum pseudozilingianum	VU	1
	Trichaptum laricinum	NT	28
	Trichaptum pargamenum	NT	6
	Tricholoma sulphurescens	NT	1
Heteroptera			5
	Aradus truncatus	NT	2
	Ceratocombus corticalis	VU	3
Hymenoptera			3
	Chrysis longula	NT	1
	Chrysis subcoriacea	NT	1
	Coelioxys lanceolata	VU	1
	Nomada moeschleri	NT	2
	Pemphredon flavistigma	VU	1
Lepidoptera			18

	Baptria tibiale subsp. *borealis*	EN	1
	Clepsis lindebergi	EN	3
	Cydia leguminana	EN	1
	Ethmia quadrillella	VU	3
	Hemaris tityus	NT	1
	Lamellocossus terebra	VU	2
	Lycaena helle	EN	2
	Merrifieldia tridactyla	EN	1
	Niditinea truncicolella	NT	2
	Nola karelica	EN	2
	Pyrausta cingulatus	EN	1
	Rhopobota stagnana	VU	1
	Xestia atrata subsp. *haraldi*	EN	1
Lichenes			39
	Acrocordia cavata	NT	3
	Alectoria sarmentosa subsp. *sarmentosa*	NT	6
	Arthonia leucopellaea	VU	2
	Arthonia ruana	NT	3
	Bacidia igniarii	VU	1
	Bacidia incompta	NT	1
	Bacidia laurocerasi	EN	1
	Bryoria fremontii	NT	1
	Bryoria nadvornikiana	NT	2
	Calicium adspersum	VU	1
	Calicium salicinum	NT	1
	Chaenotheca chlorella	NT	3
	Chaenotheca gracilenta	VU	7
	Chaenotheca gracillima	NT	5
	Chaenotheca laevigata	VU	1
	Chaenotheca stemonea	VU	4
	Chaenotheca subroscida	NT	5
	Chaenothecopsis epithallina	NT	1
	Cliostomum leprosum	NT	1
	Collema furfuraceum	NT	2
	Collema occultatum var. *occultatum*	NT	1
	Cyphelium karelicum	VU	1
	Evernia divaricata	VU	2
	Evernia mesomorpha	NT	2
	Gyalecta truncigena	CR	1
	Hypocenomyce anthracophila	NT	2
	Hypocenomyce castaneocinerea	NT	2
	Leptogium saturninum	NT	17
	Leptogium subtile	VU	5
	Leptogium teretiusculum	NT	5
	Lobaria pulmonaria	NT	17

	Lopadium disciforme	NT	3
	Micarea hedlundii	VU	1
	Microcalicium arenarium	NT	1
	Nephroma bellum	NT	12
	Nephroma resupinatum	NT	9
	Parmeliella triptophylla	NT	11
	Peltigera horizontalis	NT	2
	Phlyctis agelaea	EN	1
	Protopannaria pezizoides	NT	7
	Ramalina thrausta	VU	2
	Sclerophora coniophaea	NT	2
	Sclerophora peronella	VU	1
	Usnea glabrescens	NT	1
Mammals			17
	Lynx lynx	VU	1
	Pteromys volans	VU	16
Mollusca			11
	Bulgarica cana	EN	3
	Macrogastra plicatula	NT	6
	Vertigo genesii	EN	2
Plecoptera			2
	Nemoura dubitans	VU	2
Trichoptera			3
	Crunoecia irrorata	EN	2
	Ecclisopteryx dalecarlica	VU	1
Vascular plants			131
	Antennaria dioica	NT	1
	Arnica angustifolia	EN	2
	Asplenium ruta-muraria	EN	7
	Botrychium boreale	VU	1
	Botrychium lanceolatum	VU	4
	Botrychium lunaria	NT	25
	Botrychium multifidum	NT	5
	Calypso bulbosa	VU	27
	Campanula cervicaria	VU	4
	Carex atherodes	NT	1
	Carex heleonastes	VU	2
	Carex paniculata	EN	1
	Carlina biebersteinii	EN	1
	Cerastium alpinum (Keski-Lapin serpentiinirodut)	NT	2
	Chimaphila umbellata	NT	1
	Crepis tectorum subsp. *nigrescens*	EN	1
	Cypripedium calceolus	NT	26
	Dactylorhiza incarnata subsp. *cruenta*	VU	1
	Dactylorhiza incarnata subsp. *incarnata*	VU	7

Dactylorhiza traunsteineri	VU	1
Dianthus deltoides	NT	2
Drosera intermedia	VU	1
Elymus fibrosus	VU	3
Epilobium laestadii	EN	4
Epipactis atrorubens	VU	9
Epipogium aphyllum	VU	3
Erigeron acris subsp. *decoloratus*	VU	8
Eriophorum brachyantherum	VU	1
Gymnadenia conopsea var. *conopsea*	VU	4
Gymnocarpium continentale	NT	1
Hammarbya paludosa	NT	3
Kobresia simpliciuscula	EN	1
Lonicera caerulea	EN	3
Lychnis alpina var. *serpentinicola*	NT	2
Minuartia biflora (serpentiinityypit)	NT	1
Potentilla chamissonis	NT	1
Rhynchospora fusca	NT	1
Salix pyrolifolia	CR	2
Saxifraga hirculus	VU	15
Schoenus ferrugineus	EN	4
Silene tatarica	VU	3
Thymus serpyllum subsp. *serpyllum*	NT	12
Viola persicifolia	EN	1
Woodsia glabella	NT	1

Paper III SI: Appendix S3

Distribution analyses of threatened species.

Methods

Taxon distributions were assessed using maximum entropy modeling (MaxEnt version 3.3.3, http://www.cs.princeton.edu/~schapire/maxent/). Each taxon was modeled as a whole (White et al. 2012), and all the species of the specific taxon were simultaneously included to the model. MaxEnt is a machine-learning based method, which has been used extensively in ecological studies to model species' distributions in relation to the physical environment, and is considered to work well with presence-only data and small sample sizes (Elith et al. 2011; see Phillips et al. 2006, for a detailed description of this technique). MaxEnt analyses were performed with two types of datasets, to limit the possible effect of sample selection bias (where some areas of the study site are sampled more intensively than the others; Kramer-Schadt et al. 2013). For this, we used both the datasets used in the biodiversity models: the full data and the sampled data with far fewer absence-cells.

As with the threatened species richness models, MaxEnt models were run separately for eight taxonomic groups: vascular plants, fungi, lichens, beetles, bryophytes, butterflies and moths, molluscs and mammals. The data were split geographically into evaluation and calibration datasets, as described for the threatened species richness models. In order to avoid over-fitting and to achieve optimal model complexity (Phillips & Dudik 2008; Radosavljevic & Anderson 2014), the models were run with different regularization multiplier values (0.001, 0.01, 0.05, 0.1, 0.5, 1, 2 and 5). The feature classes we used in the models were linear, quadratic and product features. Otherwise, the default settings of MaxEnt were used.

The performance of each model was compared and evaluated by using AUC – the area under the receiver operating characteristic curve. Depending on the AUC value, the model can be considered excellent (AUC > 0.90), good (0.80–0.90), fair (0.70–0.80), poor (0.60–0.70) or failed (< 0.60) (Swets 1988). The model with the highest evaluation data AUC value was considered the best performer. The importance of each environmental variable in each model was assessed using its percent variable contribution (relative contribution).

Results

The results from modeling the aggregate distribution of threatened species were qualitatively similar to those for modeling threatened species richness (Table S3.1). Again, climate variables dominated, especially when using the full dataset, and the roles of topographic and geodiversity variables were greater when the most inappropriate cells for threatened species

were removed by only retaining absences adjacent to presences. The performance of all the full data models was either 'good' or 'excellent' (AUC value > 0.8).

GDD was the most important predictor across taxa in most cases, especially in models using the full dataset, except for threatened butterflies and moths for which mean precipitation was dominant. When using the full dataset, the second most important predictor was almost always also climatic. Of the geodiversity measures, the number of hydrological features was important for Lepidoptera, vascular plants (for both of which it was the strongest predictor when using the sampled dataset), bryophytes and to a lesser extent molluscs. The number of soil types was quite important in predicting the distribution of threatened beetles and mammals. Geomorphological richness was important for threatened bryophytes and lichens, and to a lesser extent beetles. Rock type richness was quite important for threatened mammals and to some extent for vascular plants, fungi and lichens.

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[Appendix S3 continues Overleaf…]

Table S3.1. A summary of model performance and dominant geodiversity (GD) and non-geodiversity (Non-GD) predictors for each species group[a] from MaxEnt modelling when the data is full (F) and sampled (S), with the greatest contributing predictor per taxon indicated (*).

	Data used (n cells)	AUC[b]	Non-GD predictor with highest percent variable contribution (%)	Non-GD predictor with second highest percent variable contribution (%)	GD predictor with highest percent variable contribution (%)	GD predictor with second highest percent variable contribution (%)
Bryophytes	F (6571)	0.869	GDD (50.4 %)*	MP (9.5 %)	GM rich (15.8 %)	Hydro rich (14.2 %)
	S (191)	0.380	–	–	–	–
Beetles	F (6571)	0.978	GDD (44.1 %)*	MP (41.3 %)	Soil rich (4.7 %)	GM rich (2.0 %)
	S (110)	0.616	ER (32.0 %)*	GDD (17.1 %)	Soil rich (16.8 %)	GM rich (14.6 %)
Fungi	F (6571)	0.825	GDD (78.3 %)*	ER (5.2 %)	Rock rich (3.6 %)	GM rich (3.4 %)
	S (593)	0.423	–	–	–	–
Lepidoptera	F (6571)	0.920	MP (40.9 %)*	GDD (39.8 %)	Hydro rich (7.9 %)	GM rich (2.6 %)
	S (66)	0.757	GDD (16.0 %)	ER (8.4 %)	Hydro rich (37.3 %)*	Soil rich (13.3 %)
Lichens	F (6571)	0.984	GDD (50.4 %)*	MP (44.3 %)	Rock rich (3.2 %)	GM rich (2 %)
	S (102)	0.769	GDD (36.6 %)*	ER (3.8 %)	GM rich (36.2 %)	Soil rich (12.8 %)
Mammals	F (6571)	0.971	GDD (84.5 %)*	MP (4.9 %)	Soil rich (4.4 %)	Rock rich (1.2 %)
	S (64)	0.759	ER (13.1 %)	GDD (12.2 %)	Rock rich (25.5 %)*	Soil rich (25.4 %)
Molluscs	F (6571)	0.955	GDD (88.7 %)*	MP (4.9 %)	GM rich (3.4 %)	Rock rich (0.1 %)
	S (45)	0.730	GDD (43.5 %)*	MP (14.3 %)	Hydro rich (14.7 %)	Rock rich (12.5 %)
Vascular plants	F (6571)	0.867	GDD (50.8 %)*	MP (20.7 %)	Hydro rich (9.6 %)	Rock rich (7.8 %)
	S (319)	0.616	GDD (25.3 %)	ER (23.6 %)	Hydro rich (27.7 %)*	Rock rich (3.6 %)

[a] See Table 1 for the explanation of variable abbreviations. All the predictors had greater values in presence cells than absence cells, except that, for beetles and fungi, geomorphological richness was significantly lower ($p<0.05$, Mann–Whitney U-test) in cells with threatened species than those without.

[b] The area under the receiver operating characteristic curve for the evaluation data, which was used for the evaluation of model performance. If AUC value was below 0.6 (i.e. failed model performance), no further results are presented.

Paper III SI: Appendix S4

Derivation of geomorphological richness: a detailed description

Observations of geomorphological features (i.e. landforms) from 2083 1-km^2 grid cells were made by an expert geomorphologist closely examining a combination of geomorphological maps (1:50,000 scale) and aerial photographs (~30 cm resolution), systematically. This mapping of landforms included all of the 22 geomorphological sub-regions of Finland (Fogelberg and Seppälä, 1986). The following environmental variables were then computed using GIS data: cover of land area (m^2), geographic coordinates, elevation (mean and range), slope angle (mean and range), theoretical solar radiation (Mj cm^{-2} $year^{-1}$) (mean and range) and topographical wetness index (TWI) (mean and range). Topographic variables were computed from a digital elevation model (resolution = 25 m) using ArcGIS 10.2. The cells were randomly allocated to calibration (n=1458) and evaluation (n=625) sets. While this random approach probably overestimated the goodness of the model in model evaluation, it ensured that the calibration data included observations from all different parts of Finland and across the 22 geomorphological sub-regions. Geographical split of data would have excluded some of the geomorphological regions from the calibration data.

Geomorphological richness values were generated for all 6571 grid cells in our analyses using the geomorphological distribution modeling approach (Hjort and Luoto, 2013). The number of different geomorphological feature types in each grid cell in the calibration dataset was modeled using generalized additive modeling (GAM). GAMs are semi-parametric extensions of generalized linear models in which the linear explanatory variable is substituted with a smoothing function that can take various forms (Hastie and Tibshirani, 1990). GAMs have been found to perform very well in predictive modeling in geomorphological studies (Hjort and Luoto, 2013). Models were built using the statistical package R version 2.14.2 with standard *gam* functions in the *mgcv*-library (R Development Core Team, 2014). Model optimization was based on a backward elimination approach and the Bayesian information criterion. Based on the exploration of model residuals, a Gaussian distribution with an identity link function gave the best outcome. The environmental variables were fitted to the response using a smoothing spline with the degrees of freedom permitted to vary between one (i.e. straight-line relationship) and three (i.e. nonlinear relationship). The final calibrated GAM included the cover of land area (m^2), latitude, mean elevation, mean and range of slope angle and mean and range of TWI variables. The evaluation of the final GAM included assessment of the realism of fitted environmental variables (from exploration of the response curves), multicollinearity (variance inflation factor < 5) the model's fit to data ($r_{calibration}$=0.675),

characteristics of residuals (acceptable homoscedasticity and normal distribution according to Kolmogorov–Smirnov test), predictive performance on the evaluation data ($r_{evaluation}$=0.676; the accuracy of the model was rather good i.e. fitted line was close to the optimum fit, with intercept=0 and slope=1), and cartographical exploration of the predictions across Finland. Finally, the GAM was recalibrated using full range of observations (n=2083) and the recalibrated model was used to generate geomorphological richness values for the grid cells in our study.

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PAPER IV: SUPPORTING INFORMATION

Paper title: Modelling common and rare plant diversity and distributions in relation to geodiversity in an upland landscape

Paper IV SI: Summary

All SI, including purely digital material not provided below**, can be accessed via:

https://www.dropbox.com/s/r81j86asojcyt3q/JJB_2017_PhD_SI.zip (password: cGZdzP6Ze8).

Appendix S1: Hydrology of the Cairngorms National Park

Appendix S2: Further information on the Cairngorms National Park

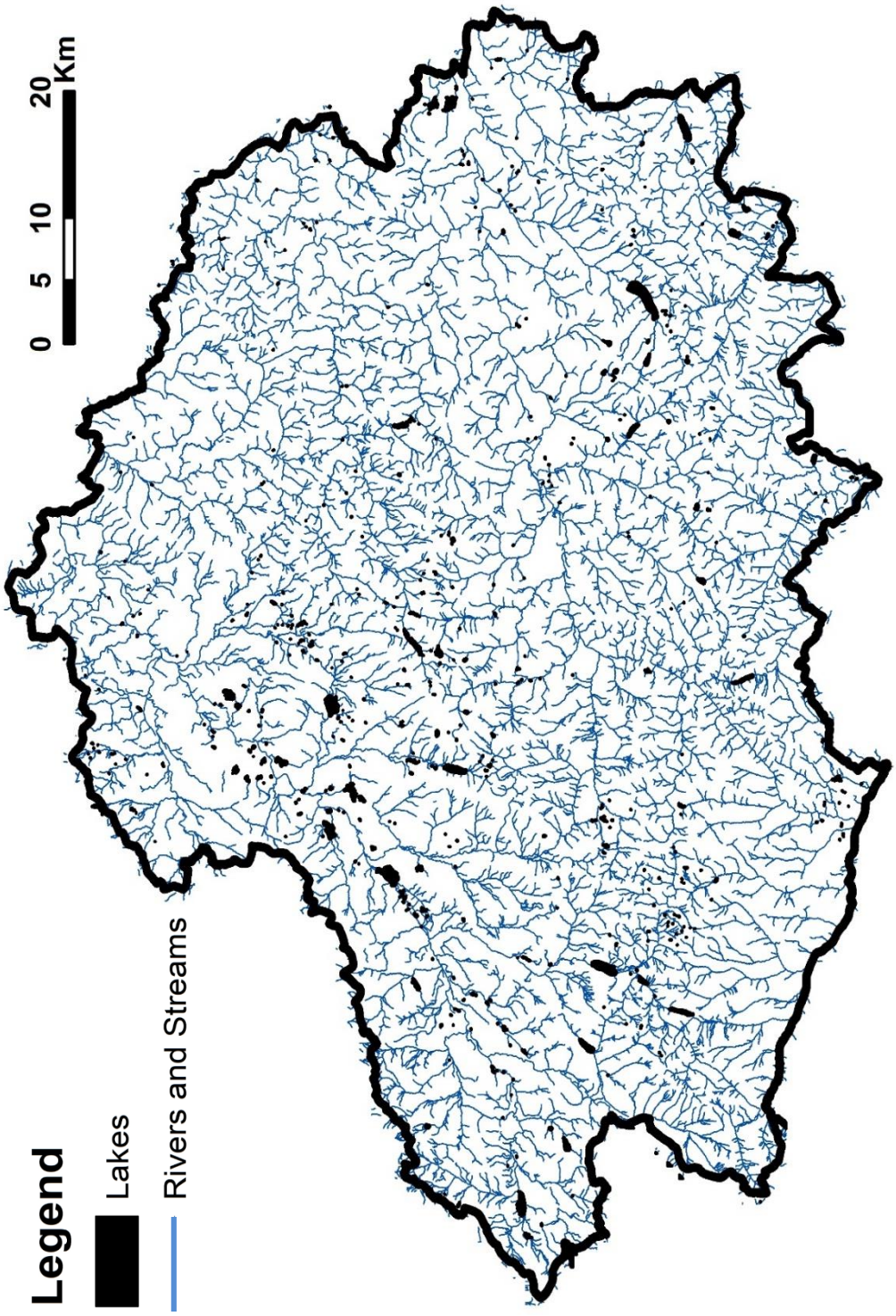
Appendix S3 (caption): Excel file containing detailed results **

Appendix S4 (caption): Full versions of Figure 3 **

Appendix S5 (caption): As S4, but for models using soil PM texture **

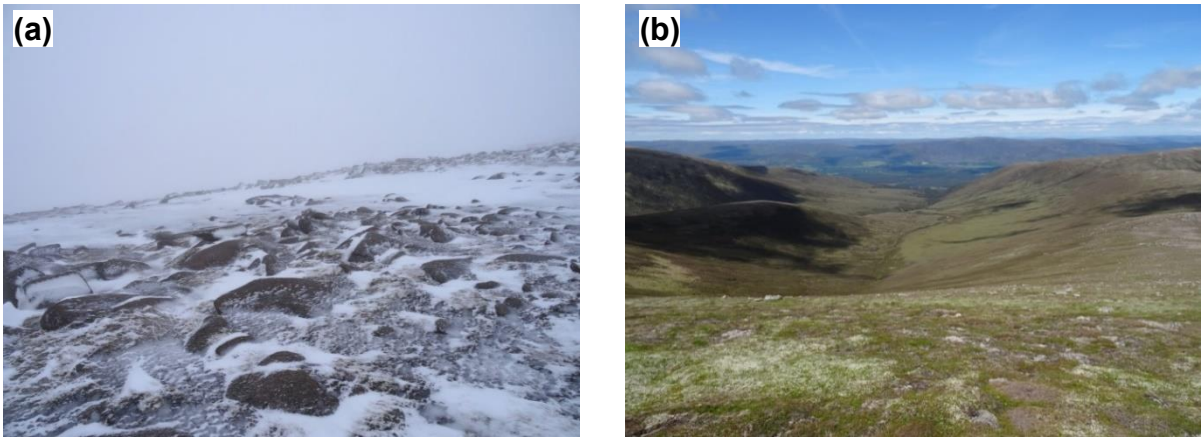
Paper IV SI: Appendix S1

Hydrology of the Cairngorms National Park



Paper IV SI: Appendix S2

Further information on the Cairngorms National Park



Photographs were taken in two different locations within the Cairngorms National Park at two times of the year, showing the diverse annual climatic conditions that the flora and fauna face. **(a)** Nearing the summit of the mountain Cairn Gorm (photograph taken at altitude of ~ 1, 150 m) in winter, the mountain after which the national part is named (January, 2016). **(b)** Looking approximately north-west and standing downslope of Sgòran Dubh Beag in the Invereshie and Inshriach National Nature Reserve (June, 2013). © Joseph J. Bailey.

The Cairngorms National Park in the Central Highlands of Scotland. It is the highest area in Great Britain and is broadly illustrative of British upland landscapes. Additionally, the Cairngorms contains four of the five largest mountains in the UK; there are 52 summits over 900 m Britain's upland landscapes are often inherently geodiverse areas, with intricate geological and hydrological features and complex topographies. However, they have been impacted by humans since deforestation in Neolithic times, with more recent activities including tourism and intensive management for agriculture, grouse hunting and deer stalking: these activities can be beneficial but excessive burning of heath and grass can degrade affected areas (Burt et al., 2002). Meanwhile, grazing is a widely-reported issue in relation to hampering the growth of native flora (JNCC, 2002; Medina-Roldán et al., 2012; Moore and Crawley, 2014; Ross et al., 2016), as is the sensitivity of peat, which is important in the context of carbon storage and climate change (Worrall et al., 2003; Evans and Warburton, 2010).

The Cairngorms was largely formed during the Caledonian Orogeny from the late-Silurian to the early-Devonian (~ 425 Ma) and the area is formed of a granite pluton created by at least two intrusions, which contains mostly quartz and feldspar (Gordon and Sutherland, 1993; Hall et al., 2013). The present geomorphological assemblages are typical of a once-glaciated mountain area, with glacial erosion generally confined to the valleys and corries,

dissecting the uplands (Hall et al., 2013). There are also many pre-glacial and non-glacial landforms, as well as those resulting from glacial erosion or deposition. The first glaciation of the Cairngorms was approximately 2.6 Ma, after which alternating glacial and periglacial conditions ensued (Clapperton, 1997; Hall et al., 2013). Pre-glacial landforms are extensive and include paleosurfaces and breaks of slope, topographic basins, valleys (the main valleys predated the Pleistocene), domes, and tors (detailed by Hall et al., 2013). Glacial landforms are marked by sudden breaks from the gentler pre-glacial mountain forms and include corries and roches moutonnées, as detailed by Sugden (1968) and Gordon and Sutherland (1993), alongside periglacial features such as rock glaciers and boulder fields.

Deer are common and form an important part of the area's heritage. However, high numbers prevent native woodland regeneration and can negatively impact fragile habitats such as moss and lichen heaths and blanket bogs (Edwards & Kenyon, 2013). The 'rewilding' of various fauna, which are and will impact the existing species, presents an ongoing discussion in the Cairngorms, and the UK's uplands more generally (e.g. see Sandom et al., 2013).

In terms of human presence, about 16,000 people currently live in the Cairngorms across several lower-altitude settlements and isolated properties. Meanwhile, tourism accounts for 80% of the economy and there are thought to be around 1.4 million visitors to the area every year (Visit Cairngorms, 2016).

References for Appendix S2

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Paper IV SI: Appendix S3 (caption)

Excel file containing detailed results

Results are detailed on a species-by-species basis in this '.xlsx' Excel file. Note the tabs along the bottom, splitting the results according to soil texture properties versus those using mineralogy. Some pivot tables have been created under the third tab. The species diversity results are on the top two data rows (rows 2 and 3) and are shaded blue; all other results are on a per species basis.

Edited caption reminder for Figure 3 in the main text

Model statistics and model contributions from model predictors for models of species diversity (one model for common and one for rare species) and species' distributions (results across models for each individual species) for all common (green, **always on left**) and rare (blue, **always on right**) species across the whole of the Cairngorms National Park. […] Model fit (SS) and evaluation (CV) statistics have been multiple by 100 for purposes of plotting. […] Model contributions have been combined for each predictor set (see Table 1). **Appendix S4** shows results for each individual area and **Appendix S5** is as **Appendix S4** but shows the results when soil parent material texture was used instead of mineralogy

Paper IV SI: Appendix S4a (caption)

Full version of Fig. 3a

As Fig. 3a but for the north, east, south, and west (see Fig. 2) as well as the whole area. The figure is less detailed, though. The left of the black lines per model statistic (SS and CV) or predictor is always for common species diversity, and the right for rare diversity. Absolute model contributions to the model are shown (0 – 100%).

Paper IV SI: Appendix S4b (caption)

Full version of Fig. 3b

As Appendix S4a, but negative values are considered whereby if a predictor had a negative relationship with species richness, this is reflected in the model contribution.

Paper IV SI: Appendix S5a (caption)

As S4a, but for models using soil PM texture

As Appendix S4a, but using model results where soil parent material (PM) texture coverage and variety was used instead of soil PM mineralogy.

Paper IV SI: Appendix S5b (caption)

As S4b, but for models using soil PM texture

As Appendix S4b, but using model results where soil parent material (PM) texture coverage and variety was used instead of soil PM mineralogy.

FINIS