Understanding trait diversity: The role of geodiversity

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Highlights

- Geodiversity, the abiotic heterogeneity of the Earth’s surface and subsurface, is gaining recognition for its links to biodiversity and community assembly; however, geodiversity’s relationship with trait diversity is poorly understood.
- The ecological niche is at the core of geodiversity–trait diversity relationships; investigating patterns between geodiversity and trait diversity can provide mechanistic inferences relating to community assembly and, in turn, improve biodiversity predictions and ecological niche models.
- Modern data availability and analytical tools provide novel opportunities for nuanced and fuller characterisation of geodiversity–trait diversity relationships across broad extents.
- Current research indicates that specific geodiversity components are important drivers of multivariate trait diversity, while other components elicit strong trait-specific responses.

Keywords

abiotic heterogeneity; applied ecology; geodiversity; trait diversity; niche.

Abstract

Geodiversity – the abiotic heterogeneity of Earth’s (sub-)surface – is gaining recognition for its ecological links to biodiversity. However, theoretical and conceptual knowledge of geodiversity–trait diversity relationships is currently lacking and can improve understanding of abiotic drivers of community assembly. Here we synthesize the state of knowledge of these relationships. We find that some components of geodiversity (e.g. topographic heterogeneity) elicit strong trait responses, while other components (e.g. substrate heterogeneity) have marginal effect in driving trait distributions. However, current knowledge is lacking in key aspects, including geodiversity's effect on trait-specific diversity and intraspecific variation. We call for the explicit inclusion of geodiversity when relating environmental drivers to trait diversity, taking advantage of the increasing availability of trait and geodiversity data.

Geodiversity: A stage for form and function

Heterogeneity of the Earth's abiotic surface and subsurface is increasingly recognized as a driving factor influencing the distribution and diversity of biological communities [1]. Earth's abiotic surface and sub-surface can be divided into four major categories: geology (e.g. rocks and minerals), geomorphology (e.g. landforms and topography), hydrology (e.g. fluvial processes), and soil (e.g., chemical composition). Following well-established convention, we use '**geodiversity**' (see Glossary) as an umbrella term to describe heterogeneity across these four categories [2]. Geodiverse landscapes maintain diverse environmental conditions, dynamic processes, abiotic resources, and refugia for organisms to exploit [3, 4]. This can lead to increased community-level organismic diversity [3]. Indeed, research linking geodiversity to species diversity typically supports this theory (e.g. [5-7]). These findings motivate hypotheses towards a more nuanced understanding of geodiversity's influence on ecological communities (i.e. individuals co-occurring within the same geographical area).

Understanding the degree to which geodiversity mediates communities requires knowledge of the interface that links the abiotic and biotic realms – geodiversity's capacity to drive diverse environmental responses [8, 9]. Organismal **traits** include morphological, physiological, and phenological characteristics that affect an organism's growth, reproduction and survival, and thus their response to, and effect upon, environmental conditions [10]. Consequently, measures of community trait diversity (i.e. **trait diversity**) are well suited to answering important questions on the capacity for geodiversity to elicit ecological responses by organisms. Understanding **trait responses** to abiotic heterogeneity is an established and rapidly developing field of ecology and biogeography [11], and calls for more rigorous testing of these responses have been made [8]. Research linking geodiversity to trait diversity can build upon this field by providing mechanistic/correlative inferences on abiotic drivers of community assembly and, in turn, geodiversity's capacity to predict patterns of biodiversity.

Existing perspectives have yet to provide insight into geodiversity's capacity to harbour diverse traits within and across communities. Recently, there has been a surge in research linking **geodiversity components** to trait diversity (e.g. [12-15]), which we review in depth here. We discuss theoretical mechanisms, key considerations, and refine the existing perspective on abiotic heterogeneity–biodiversity research by synthesizing current trends linking geodiversity to trait diversity.

Geodiversity and the ecological niche

Geodiversity influences the range of environmental conditions (e.g. microclimates) and abiotic resources (e.g. nutrients), potentially allowing diverse strategies of species with different traits to co-occur. In theory, geodiversity selects for organisms with specific traits via **environmental filtering** [9]. Thus, when geodiversity is greater, we would expect to observe a broader range of trait responses within communities through mechanisms such as climatic refuges, resource partitioning and physiological requirements leading to stabilised **co-occurrence** between organisms possessing dissimilar traits [16].

The **ecological niche** is central for a mechanistic understanding of geodiversity–trait diversity relationships. As geodiversity captures the range and diversity of abiotic components, it should represent a highly relevant axis for driving niche differences [17]. Here, we use Hutchinson's definition of the ecological niche as a multidimensional attribute of organisms expressed through the environment rather than an aspect of the environment itself. Traits determine an organism's physiological limits within niche space [18]. The extent to which niches are diversified across communities may be, at least partially, dependent on geodiversity because niche overlap is reduced by greater trait dissimilarity in geodiverse sites. Research linking geodiversity to trait diversity could thus inform niche predictions (ecological niche models, box 1), providing location-specific information on the ecological relevance of geodiversity components for many species.

A trait-based approach

A common question is: what can trait diversity tell us that species diversity cannot? Systems with high species diversity do not necessarily maintain high trait diversity because species diversity fails to capture the range of interactions that organisms have with their environments [19]. Traits can circumvent this to some degree. For example, leaf area in plants is linked to climatic stress and resource uptake [20]. Animals with different feeding habits have different resource requirements influencing food webs differentially. Body size and flight period in winged insects vary depending on abiotic refuge influencing pollination patterns [21]. Consequently, communities with high trait diversity fulfil a wider range of environmental interactions that can in turn influence ecosystem-level patterns (e.g., stability, functions [22]).

The past decade has seen considerable growth in trait databases, improving our ability to quantify trait diversity from distribution data. For example, TRY provides data on plant traits such as specific leaf area for >10,000 species [23] and AVONET provides morphological measurements for >11,000 bird species [24]. In geodiversity–trait diversity research, community-level trait diversity is measured in two ways, which we go on to discuss: 1) diversity within specific traits, and 2) multivariate diversity across two or more traits.

A trait-specific approach involves exploring trait-specific variation in relation to gradients of geodiversity. This approach provides an explicit process-based link between geodiversity and the diversity of a trait of interest. Importantly, many traits will respond to processes other than geodiversity, such as climate, competition or predation thus careful consideration, be it from theoretical expectations or research, is needed when selecting traits for trait–geodiversity research.

Linking specific traits to geodiversity has typically involved testing measures of trait variance against site-level measures of geodiversity, under the expectation that sites with high geodiversity facilitate reduced niche overlap. For example, vegetation plots with increased soil depth heterogeneity facilitated greater co-occurrence between plants with differing heights (Figure 1A) and, in turn, increased height diversity within communities (Figure 1B) [25-27]. This indicates that soil depth is linked to investment in resource-acquisition strategies by plants, with height performance varying along soil depth gradients (Figure 1C). This example seems intuitive but for geodiversity to promote co-occurrence between organisms with dissimilar traits it must not only increase relative fitness differences between organisms but also improve competitive ability so an organisms abiotic response and its capacity to compete with other organisms possessing dissimilar traits covary positively [8, 16].

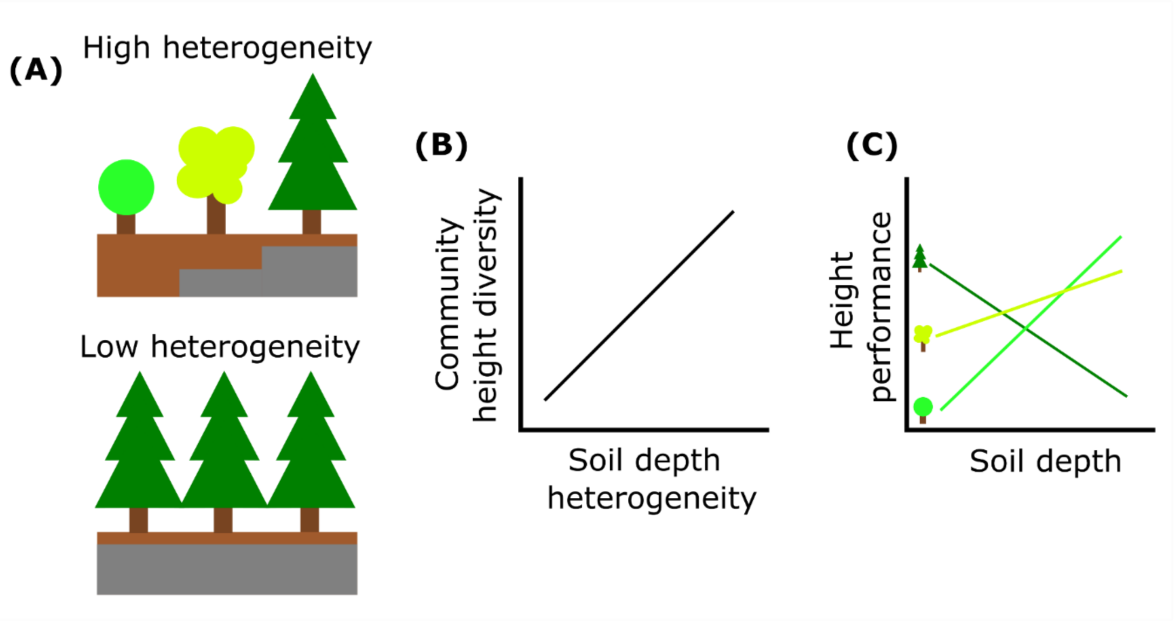


Figure 1. Conceptual figure showing a component of geodiversity (soil depth heterogeneity) driving co-occurrence between plant species of differing heights.

> Species co-occurrence is shown on two sites of high and low soil depth heterogeneity respectively (A), with expected change in community-level height diversity across sites (B). Lastly, the performance of each species with respect to height along the soil depth gradient (C).

Another means of assessing geodiversity–trait diversity relationships is through multivariate measures of trait diversity which highlight general trait patterns across communities [28]. These measures can be ascribed to **functional richness** (amount of trait space filled), **functional evenness** (abundance distribution throughout trait space) and **functional divergence** (abundance distribution at the extremes of occupied trait space) [29]. Composite measures of trait diversity are also used, including **Rao's quadratic entropy** [30] and **functional dispersion** [31], capturing information on richness and divergence. However, while measures of richness often only consider data on trait values, other measures (e.g., divergence) account for differences in species abundance reducing the risk of rare trait values having disproportionate effects on measures of trait diversity. Multivariate trait diversity can be calculated using trait x species matrices weighted by species abundance and correlated with geodiversity gradients. A common hypothesis is that higher geodiversity harbours increased functional richness and divergence due to diverse strategies expressed through traits, while functional evenness is reduced from increased likelihood of unevenness in trait abundance distributions in areas where abiotic conditions are spatially inconsistent (e.g. [32, 33]). However, measures of multivariate trait diversity typically lack information on which traits are varying along geodiversity gradients; thus, mechanistic inferences are limited compared to trait-specific approaches.

Key considerations

Trait diversity can be linked to other confounding factors such as species richness, energy availability, phylogenetic relatedness, disturbance regime and time since a community was established [34]. Such factors may create unexpected patterns of trait diversity (e.g. high trait diversity in sites of low geodiversity during succession) and so appropriate control of biotic, evolutionary and geographical factors, where possible, will reduce noise during analyses. One solution is including variables such as species richness or site-specific metadata as random effects. Alternatively, it may be appropriate to acknowledge the influence of geodiversity on, for example, species richness [5] via mediating effects influencing trait diversity in structural modelling [35]. These confounding variables have received minimal attention to date yet are potentially important to avoid misguided conclusions.

There may be a hump-shaped relationship between geodiversity and area, reflecting an area–heterogeneity trade-off [36]. That is because the most geodiverse sites may have too small an area with particular abiotic characteristics (‘effective area’) to support the persistence of populations that require those characteristics. Consequently, any research that fails to account for effective area may be observing the confounding effect of area on geodiversity–trait diversity relationships. Additionally, empirical studies of trait diversity–geodiversity relationships are limited to observations at the level of the realised niche (i.e., inclusion of biotic processes) and cannot attribute observed trait diversity solely to geodiversity or provide definitive mechanistic evidence for why observed patterns occur. Rigorous testing of mechanisms driving geodiversity–trait diversity relationships requires experimental control of confounding abiotic (e.g. climate), biotic (e.g. competition) and anthropogenic factors which can elicit similar trait responses. Such rigorous testing is currently limited [37-39].

Another consideration is the selection of appropriate traits which depends on the spatial scale of analysis (Figure 2) [40]. Generally, broad-scale geodiversity patterns may cause clustering between organisms with similar traits adapted toward the broader conditions of the environment, limiting niche overlap between communities where broad-scale geodiversity is high. At fine scales, geodiversity may determine the number of optimal and sub-optimal micro-conditions that exist for a given trait with sub-optimal conditions typically existing closer to the boundaries of an organism’s niche. In geodiverse localities, trait-level exclusion is reduced due to increased likelihood of optimal conditions being present for a given trait, leading to greater co-occurrence within communities [40] (Figure 2B). Consequently, trait selection should be tailored to the spatial scale of analysis by considering which traits are expected to vary at a given spatial scale for the geodiversity component of interest. Plants specialised to persist on distinct landforms such as cliffs and inselbergs provide an example of this scale dependency, whereby species sharing the same landform often share similar growth forms [41], however, may possess dissimilar anatomical leaf traits depending on the differing geologies and microclimates that exist locally [42].

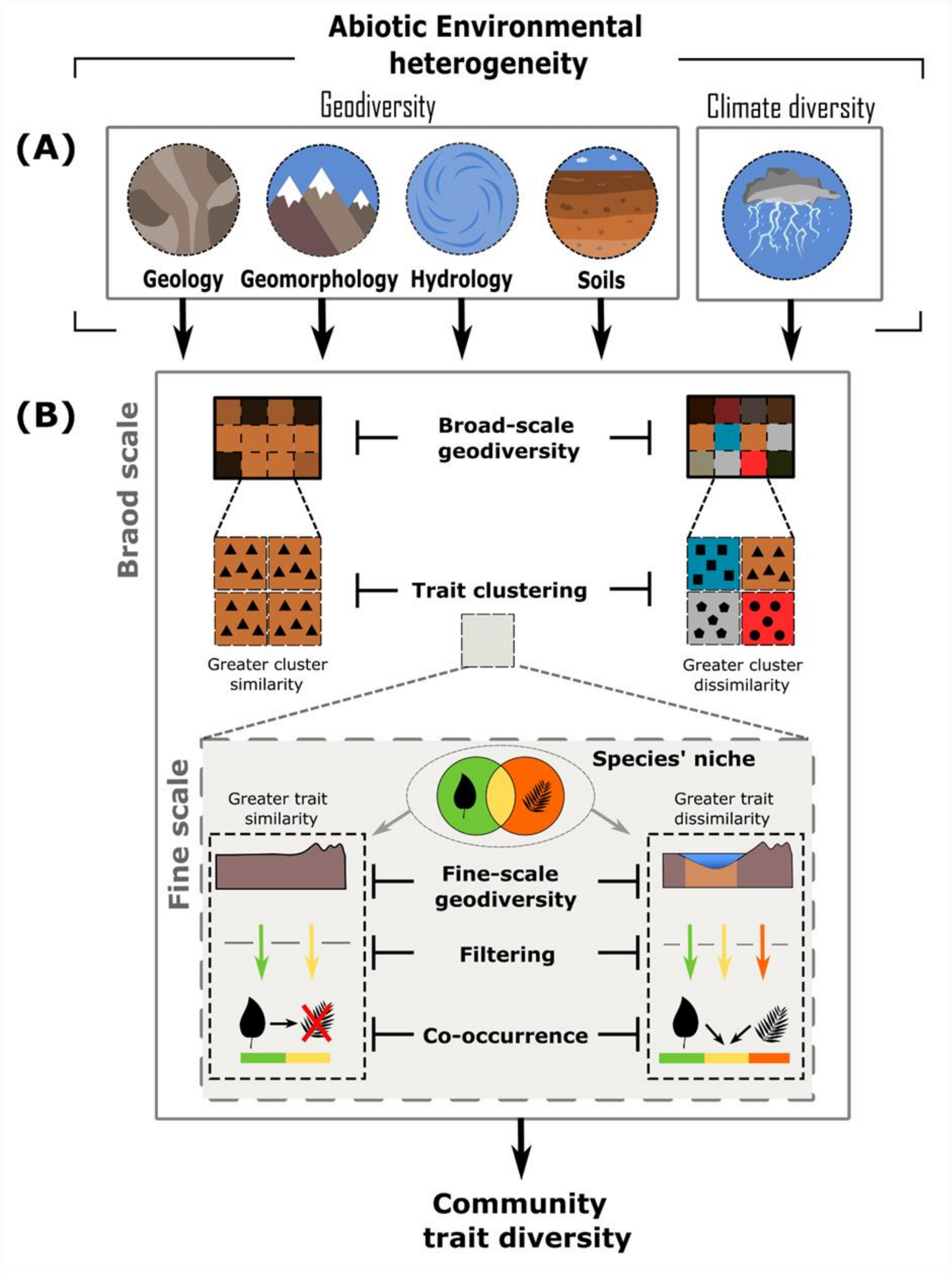

Abiotic Environmental heterogeneity
Geodiversity
Climate diversity
(A)
Geology
Geomorphology
Hydrology
Soils
(B)
Braod scale
Broad-scale geodiversity
Trait clustering
Greater cluster similarity
Greater cluster dissimilarity
Fine scale
Species' niche
Greater trait similarity
Greater trait dissimilarity
Fine-scale geodiversity
Filtering
Co-occurrence
Community trait diversity

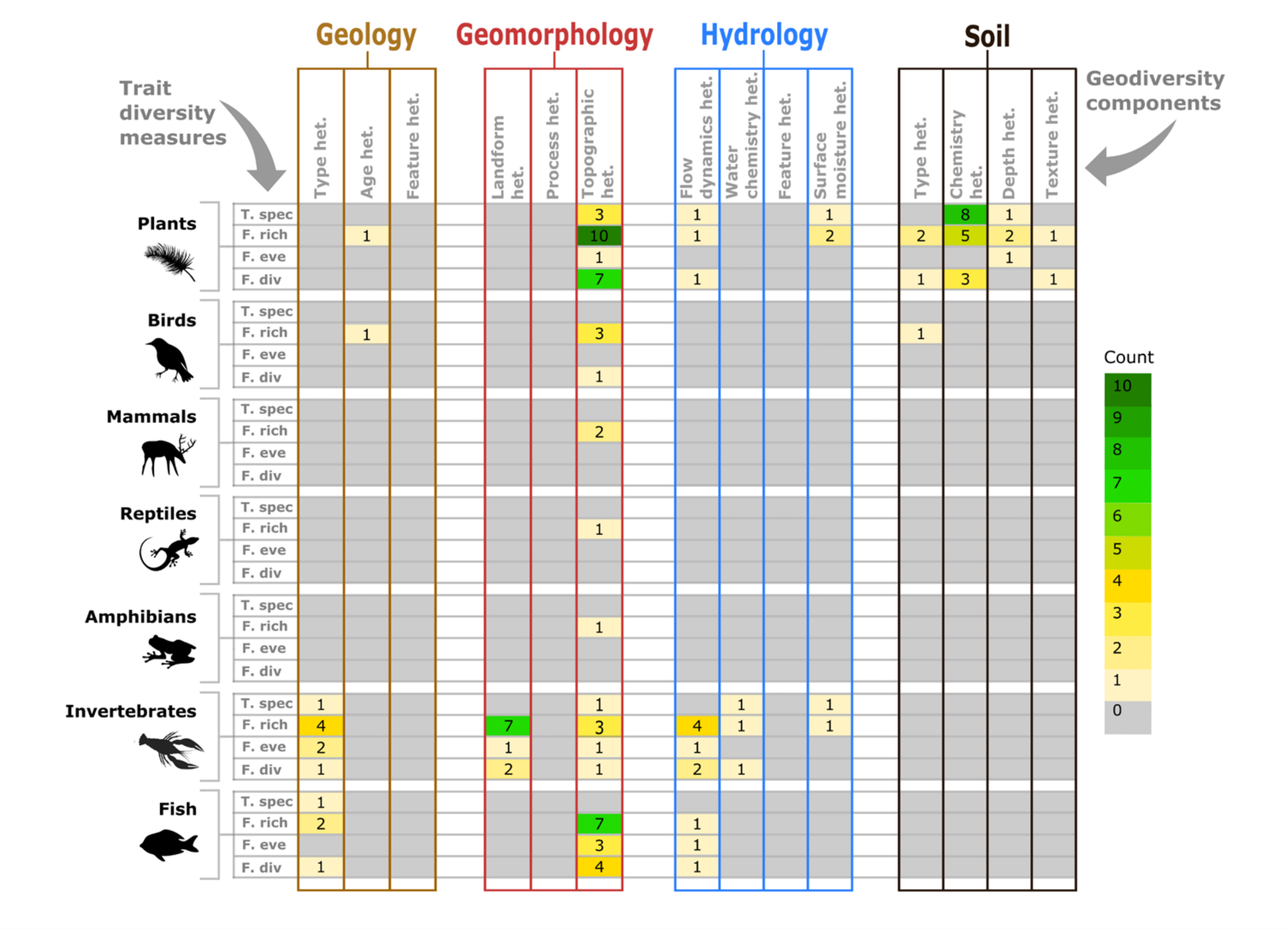
Figure 2. Geodiversity as an integral factor driving trait environment interactions across scales.

> Geodiversity is a key aspect of abiotic heterogeneity (A), which influences trait dissimilarity through broad-scale and fine-scale environmental heterogeneity (B). Geodiversity at broad-scales filters similar traits into clusters (e.g. growth forms adapted toward distinct landforms). Fine-scale geodiversity (e.g. microtopographic heterogeneity) then influences local niche overlap and in turn trait diversity by facilitating the potential for co-occurrence between dissimilar traits depending on the presence of optimal and suboptimal micro-conditions (colour coded as green, orange and yellow). Small black triangles, squares, pentagons and circles and leaf shapes indicate different traits.

Current trends linking geodiversity to trait diversity

Here, we detail findings and general trends linking geodiversity to trait diversity, and identify key research gaps by synthesising an emergent body of research (N=45 papers; see supplementary material Table S1).

For this review, we include research that has: i) quantified heterogeneity (e.g. **Shannon's Entropy** or **coefficient of variation**) within sampling units for one or more components of geodiversity; ii) where applicable, controlled for effective area [36]; and iii) focused on traits for plants or animals (across terrestrial, marine and freshwater systems). Search terms are in supplementary material S1. We extracted the number of geodiversity components and trait diversity measures considered in each article, as well as where significant correlations were found. Findings are summarised across different taxonomic groups in Figure 3. Many taxonomic groups including mammals, reptiles, birds, and amphibians, remain little-explored, compared with plants, fish and invertebrates (figure 3). Furthermore, several geodiversity components (e.g, topographic heterogeneity) have received considerably more attention than other components (e.g., landform heterogeneity).



		Geology			Geomorphology			Hydrology				Soil			
		Type het.	Age het.	Feature het.	Landform het.	Process het.	Topographic het.	Flow dynamics het.	Water chemistry het.	Feature het.	Surface moisture het.	Type het.	Chemistry het.	Depth het.	Texture het.
Plants	T. spec						3	1			1		8	1	
	F. rich		1				10	1			2	2	5	2	1
	F. eve						1							1	
	F. div						7	1				1	3		1
Birds	T. spec														
	F. rich		1				3					1			
	F. eve														
	F. div						1								
Mammals	T. spec														
	F. rich						2								
	F. eve														
	F. div														
Reptiles	T. spec														
	F. rich						1								
	F. eve														
	F. div														
Amphibians	T. spec														
	F. rich						1								
	F. eve														
	F. div														
Invertebrates	T. spec	1					1		1		1				
	F. rich	4			7		3	4	1		1				
	F. eve	2			1		1	1							
	F. div	1			2		1	2	1						
Fish	T. spec	1													
	F. rich	2					7	1							
	F. eve						3	1							
	F. div	1					4	1							

Figure 3. Heatmap illustrating aspects of geodiversity–trait diversity relationships covered in the assessed papers, across taxa, trait diversity measures and geodiversity components.

Counts refer to the number of times each geodiversity component has been investigated in the assessed papers. As some papers investigated more than one component, total counts are higher than the number of research papers considered (N=45). Trait diversity measures are as follows; T. spec: trait-specific diversity, F. rich: functional richness, F. eve: functional evenness and F. div: functional divergence. Due to their strong correlations, Rao's quadratic entropy and functional dispersion were counted as information on both functional richness and functional divergence [108]. Each unique functional diversity measure was only counted once per paper (e.g. papers that considered overlapping measures such as functional richness and functional dispersion only scored once for functional richness). "Het." under geodiversity components refers to heterogeneity.

Geomorphological heterogeneity

Geomorphological heterogeneity refers to measures of terrain ruggedness (an aspect of topography) and geomorphological typologies (e.g. landform type) as well as geomorphological processes (e.g. erosion). Under this broad definition, topographic heterogeneity represents the most widely used measure of geomorphological heterogeneity. This trend reflects the availability of global high-resolution digital elevation data and readily available indices (e.g. topographic ruggedness index [43]). These indices, however, are limited to geomorphological form and bear no explicit information on processes, composition or landform origin. High landform richness, for instance, has been linked to increased species diversity (e.g. [5, 7]), but it remains relatively unexplored at the trait level. Future research could employ landform classification tools (e.g. *r.geomorphon* [44]), which can compute landform richness from digital elevation data.

Topography is recognised for its mediating effect on environmental conditions. Climatic, hydrological and pedological gradients are influenced by topographic heterogeneity, harbouring distinct conditions at differing elevations [45]. Consequently, many taxonomic groups show increased broad-scale functional richness in response to increased topographic heterogeneity, including trees [46, 47], understory plants [14, 48-51] (though see [52]), mammals [53, 54], reptiles [54] and amphibians [54]. One potential mechanism for this pattern is isolation limiting dispersal between populations across distinct elevations. This isolating effect explains why many non-volant taxonomic groups show higher functional richness while groups able to circumvent this effect (e.g. birds with high dispersal rates) show greater trait similarity in topographically heterogenous regions [46]. Interestingly, this trend did not extend to communities within cold climates [47] due to certain elevations harbouring temperature extremes intolerant to many species. In contrast to broad-scale topographic trends, micro-topographic heterogeneity has largely been overlooked [55], despite creating diverse microhabitats which elicit trait responses from mitigating effects such as reduced climate exposure, particularly in plants [56-58].

An extensive body of work exists within marine systems which characterises geomorphological heterogeneity (usually referred to as ‘structural complexity’ or ‘seafloor ruggedness’) as a driver of trait diversity. Functionally rich and divergent communities in structurally complex systems are nearly ubiquitous [13, 59-64] (though see [65]). Increased structural complexity creates a variety of microhabitats and refuge points, diversifying strategies within marine communities [66]. Contrasting results were found for functional evenness, potentially reflecting the uneven environmental conditions harboured on structurally complex systems [33, 62, 65].

Geological heterogeneity

Geological heterogeneity refers to heterogeneity in rocks, substrate, and minerals. Some of the most speciose ecosystems in the world are found in geologically rich biomes such as tropical mountain ranges [67]. Many species, particularly plants and invertebrates, have adapted to exploit distinct substrates and mineralogies, supporting resource-acquisition and survival strategies [68]. Local-scale experiments in the Dourado river in Rio Grande do Sul (Brazil) illustrate this, finding higher macroinvertebrate trait diversity, derived from feeding habits and body size, in heterogeneous substrate treatments [39]. However, empirical research across terrestrial and marine invertebrate communities has found largely negligible results [12, 32, 33], potentially indicating that substrate heterogeneity has minimal effect in driving trait persistence once niches are realised, at least at local scales where competitive interactions are more pervasive [69, 70].

Current knowledge relating geological heterogeneity to trait diversity is limited across scales and taxa. Plant traits, for instance, are intimately linked with fine-scale abiotic resources, yet we only found one paper assessing this aspect with geological heterogeneity [46]. Regional analyses using the U.S. Geological Survey data have shown minimal significance of geological age richness on bird and tree trait diversity at 50km grain size across the contiguous USA [46]. It remains unclear whether this pattern is a product of the coarse resolution and characterisation of geological conditions used or a lack of trait response to geology-driven conditions. Future research should focus on smaller spatial extents, where fine-grained geological maps that capture ecologically relevant information are more readily available (e.g. [71]).

Hydrological heterogeneity

Hydrological heterogeneity relates to fluvial and hydrological processes and features, surface moisture, and water chemistry. Spatiotemporal heterogeneity in fluvial processes, such as flow and flooding regimes diversify disturbance levels in space and time. This allows a diverse range of survival strategies throughout communities expressed through variation in stress-tolerance traits. For instance, riparian trees exhibit greater variation in wood density in areas with increased heterogeneity in flooding rate and magnitude, improving plant tolerance to water stress [72]. Several taxonomic groups corroborate this trend, showing increased trait variation, functional richness and dispersion in response to increased heterogeneity in flow and flooding regimes. These include plants across drainage basins of Eastern Australia [73], riparian fish in the Mississippi–Ohio River, USA [74] (though see [75]), and macroinvertebrates in Finland and Norway [32]. This points toward fluvial processes widening species niches, perhaps due to community-level trade-offs between stress-tolerance and resource-acquisition traits.

Experimental manipulations of surface moisture have revealed strong responses by resource-acquisition traits in plants (e.g. leaf dry matter content [76]), and empirical research at local spatial scales corroborates these findings [25, 77]. Given the need for water uptake by plants, this is unsurprising. At the community level, one would expect heterogeneity in surface moisture to drive trait-level trade-offs, depending on how water can best be acquired (e.g. from ground water or precipitation). Depending on surface moisture levels, we would expect subsurface traits (e.g., root traits) to respond accordingly, leading to trade-offs with above-ground traits adapted for above-ground water acquisition (e.g. height), and consequently increased functional richness in areas more heterogenous in surface moisture. However, research on functional richness in temperate climates does not corroborate this theory, at least at local scales [25, 77, 78]. Other abiotic resources may be more limiting, being more pervasive in defining trait responses within temperate regions. It remains unclear whether this trend extends to drier climates where stored groundwater may be more valuable as an abiotic resource when alternative sources of water (e.g. precipitation) are scarce. More *in situ* research across biomes will greatly improve our understanding of such patterns. Further, high-resolution geospatial data of surface moisture (e.g. [79]) may prove useful for examining correlations with trait diversity across climatically distinct regions, and higher-resolution alternatives from commercial satellites are available.

Soil heterogeneity

Soil heterogeneity refers to heterogeneity in the physical and chemical properties of soil [80]. Heterogeneity in the soil layer diversifies ecological strategies for many soil-dependent taxa (e.g. plants and soil invertebrates) [40]. Spatial heterogeneity in soil chemistry (Mg, K, Ca, P, nitrate, ammonium and C/N) represents heterogeneity in the abiotic resource pool, thus driving richness in resource-acquisition traits for plants. This trend has been recognised in tropical [15] and montane systems [78], as well as in greenhouse experiments [38] though findings have been mixed for multivariate measures of trait diversity including functional richness and divergence [15, 50, 81]. Notably, resource acquisition strategies in plants are linked to both above- and below-ground traits yet measures of multivariate trait diversity have focused almost exclusively on above ground traits, overlooking below-ground traits (e.g. rooting depth) which likely vary depending on plant capacity for below-ground resource uptake. This represents a challenge moving forward as data on below-ground traits can be challenging to collect and are poorly represented in established trait databases like TRY [23] though novel frameworks for root traits have been developed [82] and databases dedicated to root traits are emerging (e.g. [83]).

Empirical research linking soil heterogeneity to trait diversity at continental extents is limited and shows conflicting results. Soil type richness was found to significantly influence functional richness across Europe [52], but not across the contiguous USA [46]. However, soil type may be too crude to capture ecologically relevant information on trait responses. Openly available databases (e,g, *SoilGrids* [84]) allow for global characterisation of heterogeneity across multiple soil properties such as nitrogen and organic carbon content [15, 78]. However, as with many geospatial datasets covering broad extents, scaling issues, static data for dynamic features, and errors and uncertainty associated with widespread data interpolation for missing values, mean that validation with local variables may be necessary for correct interpretation of such analyses [85].

Limitations and future directions

Our knowledge of geodiversity–trait diversity patterns currently relies on empirical evidence that treats geodiversity components as individual systems interacting with traits. While this approach is conceptually and analytically useful, it is an oversimplification of interactions between the abiotic and biotic realms. Topographic heterogeneity influences the steepness of hydrological and soil gradients [45]. Surface moisture, alters soil porosity and chemistry [86]. Landforms facilitate unique geologies and geomorphological processes [87]. Methods for holistically quantifying geodiversity are available both *ex-situ* (e.g. [88-92]) and *in-situ* (e.g. [93, 94]) and have been reviewed [91, 95]. Consequently, the tools necessary to characterise the dynamic nature of geodiversity patterns exist. Accounting for these dynamics analytically could be achieved using causal modelling techniques such as structural equation models to account for covariance and mediation between abiotic components [35].

The expected difference in geodiversity–trait diversity patterns across spatial scales (figure 2B) indicates which research questions should and can be addressed at different scales of analysis. Research exploring trends across broad extents is currently limited, yet a host of datasets and tools are available to address this research gap. For instance, information theory techniques (box 2) allow for efficient characterisation of geodiversity across broad extents from remotely sensed data [96].

Characterising geodiversity using information theory illuminates the potential for geodiversity and trait diversity to be computed in a similar way. For example, Rao's quadratic entropy has been used as a composite metric of trait diversity that considers both the richness and abundance of traits [30]. Similarly, information theory-based techniques (e.g. [97]) provide an avenue to compute Rao's quadratic entropy using rasterised abiotic data which considers both the dissimilarity and abundance distribution of pixel reflectance values. As a result, we might expect Rao's quadratic entropy measures of trait diversity and geodiversity to be correlated, while the magnitude of that correlation would indicate the degree to which the two factors are matched.

Trait diversity includes **intraspecific variability** (ITV) [98], and indeed high trait diversity can be exhibited by a small number of species. This would be undetected by analyses that use averaged trait values per species. At local scales, ITV may be important because subtle environmental differences facilitate broader niches and lower trait-level overlap between neighbours that may be the same species, however, current research linking ITV to geodiversity is limited (N=6). Trait-specific measures of ITV are typically simple to compute, dimensionless and can be adjusted for sample size, to avoid underestimates (e.g. coefficient of variation estimators [99]). Further, n-dimensional hypervolumes can capture ITV within multivariate trait diversity measures and this approach has been adapted to consider fitness differences within niche space [100]. Trait diversity measures that use n-dimensional hypervolumes are useful when relating trait patterns to abiotic drivers as the hypervolume is perhaps the most analytically faithful characterisation of Hutchinson's multidimensional niche [101]. Software packages to compute trait diversity from hypervolumes using trait and abundance matrices are readily available (e.g. [102]).

Concluding remarks

Our review summarises current knowledge linking geodiversity to trait diversity. Certain geodiversity components (e.g. topographic and soil chemistry heterogeneity) seem to drive increased functional richness and trait-specific diversity across communities. However, this area of research is in its infancy, and currently provides limited insight into patterns across broad extents, effects on intraspecific variability and relationships across vertebrate taxa (see outstanding questions). Future research could benefit greatly from considering confounding variables that may influence trait diversity patterns (e.g. species richness) when linking geodiversity to trait diversity. Advances in data access, statistical techniques, information theory and remote sensing provide tools for nuanced investigation of geodiversity–trait diversity relationships. Overall, geodiversity–trait diversity research has the potential to enhance our understanding of community assembly, the extent to which abiotic components drive differences in niche space and, in turn, its capacity to improve niche modelling and biodiversity predictions.

Outstanding questions

- What is the relationship between geodiversity and trait diversity across taxa when confounding geographical, evolutionary, disturbance, and biotic factors are accounted for?
- Many taxonomic groups such as birds and mammals remain underexplored in the context of geodiversity-trait diversity relationships. Given the increasing availability of trait databases for vertebrates such as AVONET (bird trait

database), can geodiversity explain trait diversity across or within communities for these taxonomic groups?

- Many components of geodiversity remain uninvestigated or poorly investigated (e.g., landform, water chemistry and feature heterogeneity). Which of these components are relevant to explaining patterns in trait diversity across taxa and temporal-spatial scales?
- Which components of geodiversity are important for intraspecific trait variation?
- Can satellite derived data and information theory capture geodiversity–trait diversity relationships across broad extents?
- Can geodiversity components compliment the BAM (biotic, abiotic and movement) framework and improve predictions in ecological niche modelling?
- How important is consideration of dynamic processes in geodiversity assessments seeing that most databases on elements of geodiversity are static, despite the highly dynamic nature of these factors?

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Additional material

Box 1

Improving ecological niche models

Ecological niche models are mathematical projections of where an organism can persist based upon environmental parameters (potential niche). These models often utilise the BAM (biotic, abiotic and movement) framework to model species' niches using ecologically relevant demographic, biological and environmental data [103]. Previously, ecological niche models have been useful for multiple reasons such as *en masse* biodiversity forecasting [104]. The abiotic component of the BAM framework has relied on climatic (climate envelopes) and landscape (e.g. habitat type) data. While relevant, these likely fail to capture all important abiotic axes for many species' niches. For instance, ecological niche modelling of species that are sensitive to geo-hydrological conditions may grossly overestimate potential niches when modelled purely on climatic data. Consequently, surface and subsurface components (geology, geomorphology, hydrology and soils) represent niche axes that may provide crucial information for more accurately modelling the potential niche of many species.

While our discussion of our review's findings does not explicitly relate to ecological niche modelling (measures of heterogeneity are not usually used as input data into ecological niche models), it does highlight relevant information regarding the sensitivity of trait diversity to geodiversity.

Widespread positive associations between components of geodiversity and trait diversity would suggest that many ecological niche models are projecting overestimated niches for many species. The increasing availability of open-access datasets covering abiotic surface and subsurface components across broad extents, at progressively finer spatial resolution (e.g. soil [84], surface moisture [79] and topographic data from, e.g., the Shuttle Radar Topography Mission), offers new possibilities for improving ecological niche models.

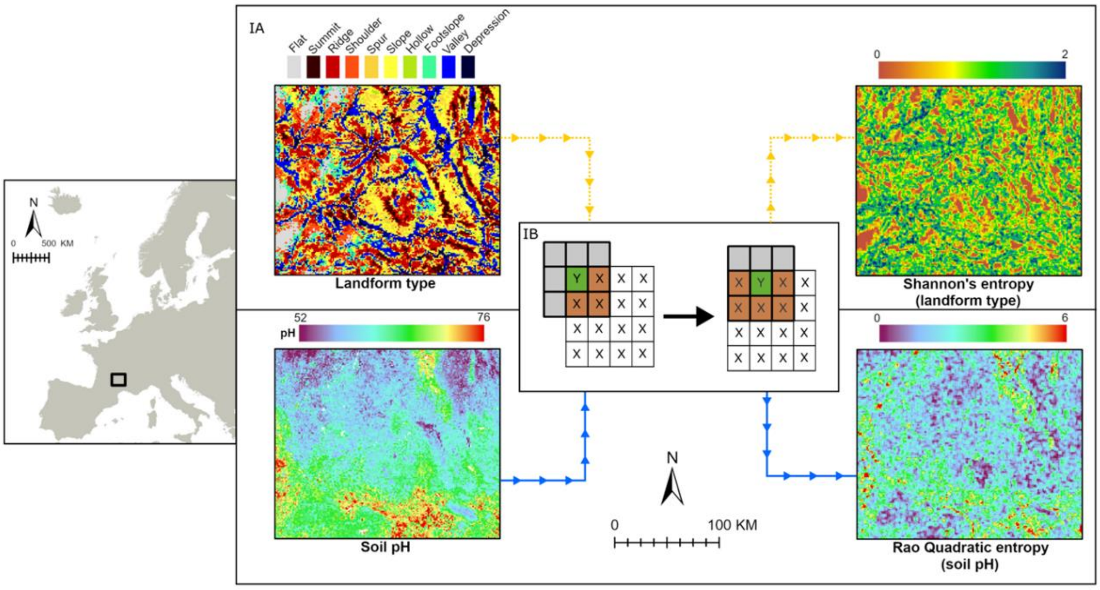
Box 2

Computing geodiversity from information theory

Remotely sensed data can provide answers to important ecological questions across broad extents using geospatial analytics [105]. In particular, raster data derived from satellite images and airborne photography provide simplified information on environmental data over large areas. From an ecological perspective, the values stored within pixels of a raster image can be used as a macroecological quantification of environmental axes in niche space, thereby providing information on abiotic resources and conditions.

Heterogeneity can be computed from environmental raster data by applying algorithms across each pixel (cells in the raster, Figure IA). This approach involves revaluing every cell with a heterogeneity measure computed using values from neighbouring cells (often named a kernel or moving window, Figure IB). This approach, while a simplification of environmental heterogeneity, offers a useful tool for characterising heterogeneity across broad spatial extents. Appropriate measures of heterogeneity depend on the type of raster data being analysed. For example, measures of Shannon’s entropy have often been applied as a measure of heterogeneity that considers the richness and abundance of pixel values [106]. However, Shannon’s entropy cannot capture the degree of difference between pixel values and so is primarily appropriate for discrete rasters (e.g. landcover types). Other measures are more appropriate for continuous data. For example, Rao’s Quadratic entropy considers the richness and abundance as well as pairwise distances between pixel values thereby preventing overvaluing of heterogeneity from similar values within a continuous raster (e.g. elevation data) [107].

Given the flexibility of the moving window approach for quantifying heterogeneity across abiotic components, and for examining the effect of scale (window size), it is a useful tool for quantifying geodiversity across broad extents. Further, once homogenised across extent, resolution (pixel size), and projection, rasters can be analysed for spatial covariance across components. Figure I provides an example of this approach used on discrete (landform) and continuous (soil pH) rasters. A point of caution is that many large geospatial datasets (e.g. *SoilGrids*, figure IA) are heavily interpolated, and thus possess uncertainties. These uncertainties should be assessed prior to use. Furthermore, consideration of the resolution is important. For example, pixels with dimensions of multiple kilometers may be too crude to capture relevant information on organisms. Lastly, moving windows are susceptible to spatial autocorrelation and so data exploration to identify non-random spatial patterns (e.g. Moran's index) are necessary to avoid misguided conclusions.



Box 2, Figure I. Example of two geodiversity components (landform type and soil pH) applied to information theory to compute heterogeneity.

IA demonstrates landform types, computed from *r.geomorphon* [44], and a soil pH raster (units are tenths of pH units) processed for heterogeneity using Shannon's entropy and Rao's Quadratic entropy, respectively. Arrows are coloured to indicate input and output of different components (yellow for landform type and blue for soil pH). IB conceptually illustrates the moving window approach applied to raster data: the moving window (3x3 shaded grey area) passes over each of the centroid pixels (highlighted in green) and computes a designated measure of heterogeneity based (Y, green pixel) upon the values of the surrounding pixels within the moving window (X, highlighted in brown). This then outputs a new raster of heterogeneity values. Elevation data were sourced from *Copernicus* and soil pH data from *SoilGrids* [84].

Glossary

Coefficient of variation

Mean divided by standard deviation. Commonly used as a measure of heterogeneity for continuous variables.

Co-occurrence

Persistence between two or more individuals within or across species within an area of interest.

Ecological niche

Position that a species exists in within multidimensional space with environmental conditions and resources as axes.

Environmental filtering

Metaphor describing the selective pressure of the environment on organisms.

Functional dispersion

Measure of multivariate trait diversity which considers the dissimilarity and abundance of traits in trait space. For functional dispersion to be high, both functional richness and functional divergence must be high.

Functional divergence

Degree to which the distribution of species abundances in trait space maximises total variation.

Functional evenness

The regularity of the distribution of abundance in trait space.

Functional richness

Amount of trait space occupied by trait values within trait space.

Trait

Morphological, physiological, and phenological characteristics that affect an organism’s growth, reproduction and survival, and thus their response to, and effect upon, environmental conditions.

Geodiversity

Umbrella term describing abiotic heterogeneity across the Earth’s surface and subsurface.

Geodiversity component

Heterogeneity of an element of the abiotic environment (e.g., soil nitrogen heterogeneity or surface moisture heterogeneity).

Intraspecific variability

Trait-level variability within one species.

Rao’s quadratic entropy

Measure of heterogeneity broadly computed from the sum of all pairwise distances between values multiplied by the relative abundance of each pair. Used as a measure of heterogeneity for continuous data.

Shannon’s Entropy

Discrete heterogeneity measure that considers the richness and abundance of values based upon there probability of appearing.

Trait diversity

Term describing the diversity of Morphological, physiological, and phenological characteristics of species across and within communities.

Trait response

Occurrence of traits in response to environmental conditions or resources.

1