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Opinion

Quantifying elemental diversity to study landscape ecosystem function

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The movement, distribution, and relative proportions of essential elements across the landscape should influence the structure and functioning of biological communities. Yet, our basic understanding of the spatial distribution of elements, particularly bioavailable elements, across landscapes is limited. Here, we propose a quantitative framework to study the causes and consequences of spatial patterns of elements. Specifically, we integrate distribution models, dissimilarity metrics, and spatial smoothing to predict how the distribution of bioavailable elements changes with spatial extent. Our community and landscape ecology perspective on elemental diversity highlights the characteristic relationships that emerge among elements in landscapes and that can be measured empirically to help us pinpoint ecosystem control points. This step forward provides a mechanistic link between community and ecosystem processes.

Highlights

Complex biotic and abiotic feedbacks affect the spatial distribution of the 25 elements necessary for life, but most studies focus on only biotic or abiotic components at small spatial extents.

Plants and animals not only affect, but also respond to the distribution and stoichiometry of elements; thus, understanding geodiversity is critical to improve our understanding of species distributions and ecosystem function.

Meta-ecosystem theory has already started to demonstrate how the feedback between biotic and abiotic components of ecosystems can impact community structure and function; however, we need an empirical parallel.

Here, we propose a framework that applies tools from community and landscape ecology to study and analyze spatial scaling of elements across landscapes. This will allow us to quantify how spatial patterns in elements vary across spatial scales.

Biotic–abiotic feedbacks connect ecosystems across landscapes

The distribution and relative abundance of the 25 **chemical elements** (see Glossary) necessary for life influence the structure and function of biological communities. However, our basic understanding of the causes and consequences of the spatial distribution of elements is limited. Historically, geological processes and abiotic factors have been the focus for predicting elemental concentrations at small, well-defined spatial **extents** (e.g., ponds) [1]. More recently, research has shed light on the significance of biotic ecosystem components, particularly biotic–abiotic feedback loops, on elemental distribution and abundance (Figure 1) [2–6]. Thus, the analyses of the spatial distribution of elements may be critical for forecasting the fate of biological communities in the Anthropocene.

Spatial patterns of elemental abundances result from combined feedbacks of passive abiotic flows and biotic ecosystem components (e.g., animal deposition of materials) acting at different spatial and temporal scales (Figure 1). At a broad spatial extent, weathering of bedrock builds an elemental pool that is then distributed via abiotic and biotic processes [7]. At smaller spatial extents, abiotic processes, such as the mixing of nutrient-rich ground water and nutrient-poor surface water, create local **elemental hotspots** or **elemental coldspots** of inorganic nitrogen (N) [8,9]. These hotspots of N can then get redistributed via abiotic and biotic processes, including daily movements of organisms (Figure 1). At small spatial extents, animals with relatively small home ranges (e.g., snowshoe hares, *Lepus americanus*, or Arctic foxes, *Vulpes lagopus*), may contribute to localized elemental hotspots [10], such as the build-up of nutrients around Arctic fox den sites [11]. Biotic processes can also operate at larger spatial scales. For example, moose (*Alces alces*) home ranges include a diversity of habitats, including early successional forests used for foraging and mature forests used for shelter. Selective herbivory by moose in foraging patches removes nutritious understory plants with relatively high N and P content [12].

Through selective foraging, moose cause a shift in the plant community to one dominated by grasses [13]. The shift in plant community alters microbial richness, decreasing the microbial nutrient mobilization and leading to forest soils depleted of N and phosphorus (P) [14], resulting in elemental coldspots across their large home ranges [15].

Abiotic and biotic drivers of elemental patterns also operate at varying spatial scales in aquatic systems [16]. Streams exhibit a large heterogeneity in nutrient concentrations, especially across short distances [17]. Some of this heterogeneity is the product of abiotic processes (e.g., surface–subsurface exchanges), while other aspects are the product of biotic processes (e.g., spatial variation in microbial activity [18]). Indeed, a study of freshwater fish in streams in Venezuela [19] demonstrated that, in specific streams, fish excretion, (biotic process) accounts for over 75% of the inorganic N in the ecosystem, particularly in the deep runs used during the dry season. Specifically, this study showed how fish distribution (over an ~2.64 km reach) can contribute to N hotspots along both spatial and temporal gradients as fish change their habitat use in response to seasonal patterns in precipitation [19]. The hotspots of inorganic N created by these fish can lead to speciose aggregations of mussels, which facilitate algal growth through N mineralization fueling adjacent terrestrial ecosystems [20,21]. These examples demonstrate

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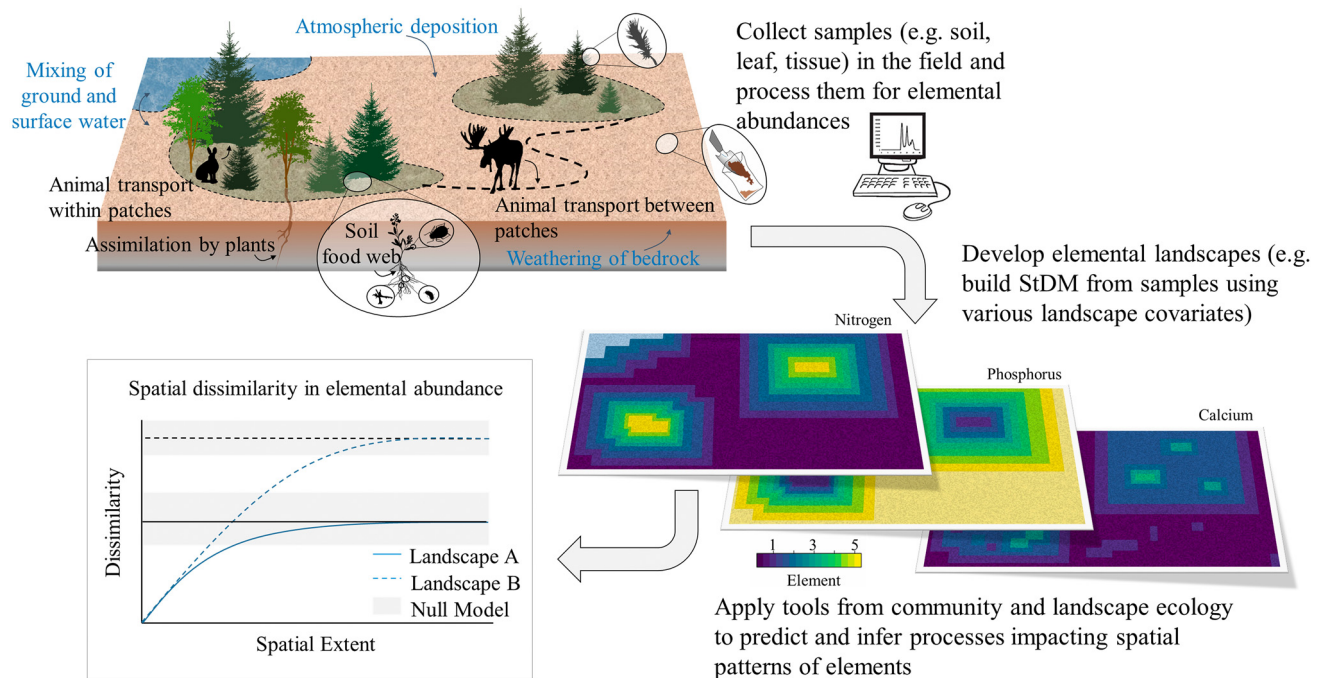
Figure 1. Using community and landscape ecology to study spatial patterns in elements. Spatial patterns of elemental abundances are the result of the combined feedbacks of passive abiotic flows (blue text) and biotic processes (black text; e.g., animal transport and deposition of materials) acting at different spatial and temporal scales. For example, at a broad spatial extent, weathering of bedrock builds an elemental pool, which then gets distributed via abiotic and biotic mechanisms. To tease out the consequences of these different processes, we propose borrowing tools from community and landscape ecology. First, data are collected at sites across the landscape from sources such as soils, plant material (e.g., forage materials), and/or animals. These samples are then processed for elemental composition. Then, an elemental landscape is created (e.g., through a stoichiometric distribution model [15]). From these landscapes, we can use techniques to summarize the spatial architecture of species diversity at increasingly larger spatial extents (e.g., the macroecological spatial smoothing approach proposed by Patrick and Yuan [30]), but focusing on elemental diversity instead. Community ecology metrics, such as β-diversity, can then be applied to integrate multiple elemental distributions and describe how these landscapes of elements are organized with increasing spatial extent. By building landscapes of elements and subsequently applying tools from community and landscape ecology, we can tease out patterns in elemental abundance that reflect the integration of geochemistry and ecosystem, food web, movement, population, and community ecology. Abbreviation: StDM, stoichiometric distribution model.

how biotic and abiotic processes can create intricate feedbacks at various spatial scales resulting in complex landscapes of elements.

Here, we propose a framework (Figure 1) to investigate the spatial scaling of elemental diversity across landscapes. We demonstrate how tools from community and landscape ecology can reveal characteristic relationships and help identify **ecosystem control points**. Investigating the spatial scaling of elemental landscapes is important because organisms both affect and respond to landscapes of elements at specific scales; thus, we end by linking elemental diversity to community structure and biodiversity. Studying and analyzing empirical patterns of elemental diversity in space, particularly across spatial grains, will provide an important first step to linking abiotic observations and biotic components of ecosystems and to assess the strength of biotic imprints on nutrient spatial heterogeneity compared with other processes. This should improve our understanding of how whole ecosystems will respond to human activities.

Tool transfer from community ecology

Critical for applying tools from community ecology to elements is the development of predictive landscapes of biologically relevant elemental diversity at regional scales, such as **stoichiometric distribution models (StDMs)** [15]. StDMs can be used to predict the spatial distribution of elements based on statistical models that correlate element distribution with environmental parameters (e.g., elevation). Instrumental to this approach is the collection of representative samples for elemental analyses at sites across the landscape (Figure 1). The type of sample collected depends on the question being asked. For example, foliage samples that represent the primary forage plant for herbivores within the community could be used as a direct measure of the bioavailable elemental concentrations for herbivores [15] and already integrate geological drivers of elemental availability. Alternatively, soil samples that represent the diversity and availability of elements for biota, including plants and microbes, could be used [22]. From these data, StDMs are constructed to extrapolate elemental composition across the landscape. As such, StDMs fill a gap in our ability to measure elements across a whole landscape and draw on the well-studied species distribution modeling literature replete with research on quality control and uncertainty in model predictions [23,24]. Alternative quantitative approaches have been developed for mapping isotopes in geographical space [25]. Similar to StDMs, **isoscape** models extrapolate isotope abundances across a landscape; however, instead of predicting abundance based on covariates (e.g., slope), isoscape models estimate abundances by allowing for both fractionating and nonfractionating processes specific to the element [25]. Nevertheless, whichever approach is used, the result is the same: mapped landscapes of elements.

Using these landscapes of elements, we can then explore patterns of relative elemental abundance at multiple spatial extents, which is a critical step because different abiotic and biotic processes act at different spatial extents. For example, leaching of inorganic nutrients from terrestrial to aquatic ecosystems [26] or the redistribution of nutrients due to migrating snow geese (*Anser caerulescens*) [27] occur at a large spatial extent, while the exchange of surface and subsurface waters at the edges of streams [17], or the recycling of nutrients by fish [19] occur at much smaller spatial extents. There are numerous techniques available from community and landscape ecology that examine the spatial architecture of species diversity [28,29] that can easily be applied to elemental diversity. One approach is **macroecological spatial smoothing (MESS)**, whereby a moving window is applied across a landscape, with the size of the window increasing incrementally to randomly subsample the landscape with increasing extent [30]. Consistent with Barton *et al.* [31], the choice of varying **grain size**, extent, or both, as well as the selected **dissimilarity metric**, change predicted relationships between dissimilarity and

Glossary

β-Diversity metrics: relate the total number of species in a set of sampling units (γ-diversity) to the average number of species in individual sampling units from the full set (α-diversity). When the diversity is accounted for as an effective number of species, β-diversity is the ratio of γ- to average α-diversity; in other cases, the relationship can be additive; examples include Whittaker's original measures of β-diversity and Shannon diversity indices.

Chemical element: chemical substance that cannot be broken down further into another substance (e.g. N, calcium), often referred to simply as an element and classified in the periodic table of elements.

Dissimilarity metrics: measures of compositional difference between two sampling units; examples include Jaccard's or Sørsensen's dissimilarity metrics.

Ecosystem control point: areas of the landscape that have a disproportionate influence on the biogeochemistry of an ecosystem incorporating both a spatial and a temporal component.

Elemental coldspots: patches that show disproportionately low concentrations of elements (or specific elements) compared with the surrounding matrix.

Elemental hotspots: patches that show disproportionately high concentrations of elements (or specific elements) compared with the surrounding matrix.

Extent: sampling area that is the aggregate of all sampling units.

Geodiversity: diversity of abiotic features and processes of the Earth's geosphere.

Grain size: base sampling unit or study resolution.

Isoscapes: maps of the spatiotemporal distribution of isotopes generated by mathematical models of isotope-fractionating processes and environmental conditions.

Local contributions to β-diversity (LCBD): contribution of sampling units (e.g., plot or grid cell) to variation in community composition across a larger area. Local contribution to β-diversity is a metric useful to identify sampling units that are unique relative to the complete set of sampling units.

Macroecological spatial smoothing (MESS): neighborhood smoothing protocol that acts as a moving window

area. Thus, care must be taken when choosing approaches. Following Patrick and Yuan [30], we suggest fixing grain and varying extent, to begin with, since there are examples within the landscape ecology literature that demonstrate the impact of grain on spatial distribution models [32,33].

Once the landscape of elements is created, and a spatial scaling approach decided upon, we can apply concepts from community ecology. These concepts describe how species are organized across space (e.g., **β-diversity metrics** [34]) and can be used analogously to explore how elements are organized across the landscape with increasing spatial extent (i.e., fixed local area, but increasing regional area) (Figure 1). Elemental composition data are akin to community composition data and, therefore, may need to be transformed (e.g., a chord transformation [35]) depending on the diversity metric chosen; see guidelines in [36]. Finally, other studies apply dissimilarity approaches to nutrients to examine other ecological questions, such as the impact of stoichiometric dissimilarity on litter decomposition [37]; here, we apply dissimilarity approaches to elemental landscapes to describe the spatial scaling of elements.

Insights from elemental dissimilarity

The benefit of using well-studied metrics from community ecology is the testable predictions that can emerge from these analyses, particularly given the research on how abiotic and biotic factors affect the scaling of species diversity [31]. More importantly, these approaches allow us to distill N-dimensional elemental landscapes into a single metric per extent. Intriguingly, different elemental distributions have distinct characteristic relationships between dissimilarity and spatial extent (Box 1), which improves our understanding of both the elemental distributions and the scales at which the abiotic and biotic processes might be strongest. For example, if elemental distributions have a predictable gradient, as might be expected from abiotic impacts, such as Saharan winds depositing nutrients in South American rainforests, we observe low dissimilarity at small extents that eventually asymptotes in dissimilarity at broad extents (Box 1). This is a trend that emerges at the landscape scale and, thus, we would expect landscape-extent abiotic and biotic processes to be key drivers of elemental distributions.

Reality is likely more complex than predictable gradients of elemental composition as described above. For example, the congregation patterns of Venezuelan stream fish in deep pools post feeding leads to patchy distributions of N and P [19] and a characteristic dissimilarity curve with increasing spatial extent (Box 1). This pattern demonstrates that abiotic and biotic processes operating at smaller spatial extents may be dominant drivers. Alternatively, foraging movements of large animals may result in more homogeneous, or random, elemental distributions in some ecosystems (Box 1; Figure 1C). For example, the active foraging of large grazers in the Serengeti grasslands likely disperses elements because these large grazers recycle a large amount of fecal nutrients as they move between patches [38].

Identifying ecosystem control points

Traditional dissimilarity metrics allow us to describe differences between communities, while new approaches have taken this one step further using a metric called **local contribution to β-diversity (LCBD)** [36] to tease out the uniqueness of communities within a landscape. From an elemental standpoint, the LCBD approach allows us to identify ecosystem control points (i.e., cells that contribute more or less to elemental diversity) [39]. For example, cells with a high LCBD may be rich in a limiting nutrient or poor in an abundant nutrient. Applying an LCBD analysis across spatial extents makes it possible to see how patches of high contributions to dissimilarity form and dissipate depending on the spatial scale (Figure 2). For example, at large spatial extents, grid cells with high LCBD may concentrate around water bodies in terrestrial systems, likely driven

for visualizing and analyzing community patterns at landscape scales. In particular, the MESS approach avoids the modifiable areal unit problem that arises when researchers assign their sites into similar zones as opposed to letting the zones emerge from the data by randomly resampling a set number of cells within the windows a set number of times.
Stoichiometric distribution models (StDMs): statistical models that correlate the spatial distribution of elements and environmental predictors (e.g., slope or net primary production) across the landscape. StDMs can be used to map a predicted distribution of elements across continuous space.
Stoichiometry: balance of multiple chemical elements in living systems.
Zoogeochemistry: animal–element interactions or feedbacks that affect ecosystem elemental stocks and flows.

## Box 1. Characteristic signatures of elemental distributions

The relationships between spatial extent and elemental dissimilarity have distinct characteristic signatures, giving us the potential to tease out the scale of biotic and abiotic drivers of elemental distributions and hypothesize some drivers.

If elements are randomly distributed across the landscape, dissimilarity has a negligible change with extent since the likelihood of sampling novel elemental compositions does not change as extent increases (Figure IA). This trend emerges at the finest spatial extent, as may be expected if small-scale abiotic and biotic processes are important (e.g., microbial and fungal activity).

If elements are patchily distributed across the landscape, dissimilarity is still low at small spatial extents; however, there is a steeper relationship between spatial extent and dissimilarity and asymptotes at a much smaller spatial extent (Figure IB). Additionally, we observe a high degree of variability in element dissimilarity at smaller spatial extents, becoming less variable as extent increases. This trend emerges at smaller spatial extents, suggesting that abiotic and biotic processes operating at smaller spatial extents (e.g., mixing of surface and subsurface waters or selective foraging by consumers) are important.

If elements have even gradients across the landscape moving from high abundance to low abundance with latitude (Figure IC), dissimilarity will be low at small spatial extents, increasing and eventually plateauing at a much higher value at large spatial extents. This is a trend that emerges at large extents, suggesting that landscape-level abiotic and biotic processes (e.g., weathering of bedrock or animal migration) are important.

Using a real landscape (Figure ID) and comparing to a randomized null model, we can see that the real landscape exhibits patchy distributions of elements. This is further indicated by the large amount of variation observed between locations in the landscape, variation that is far greater than the variability introduced from the stoichiometric distribution model.
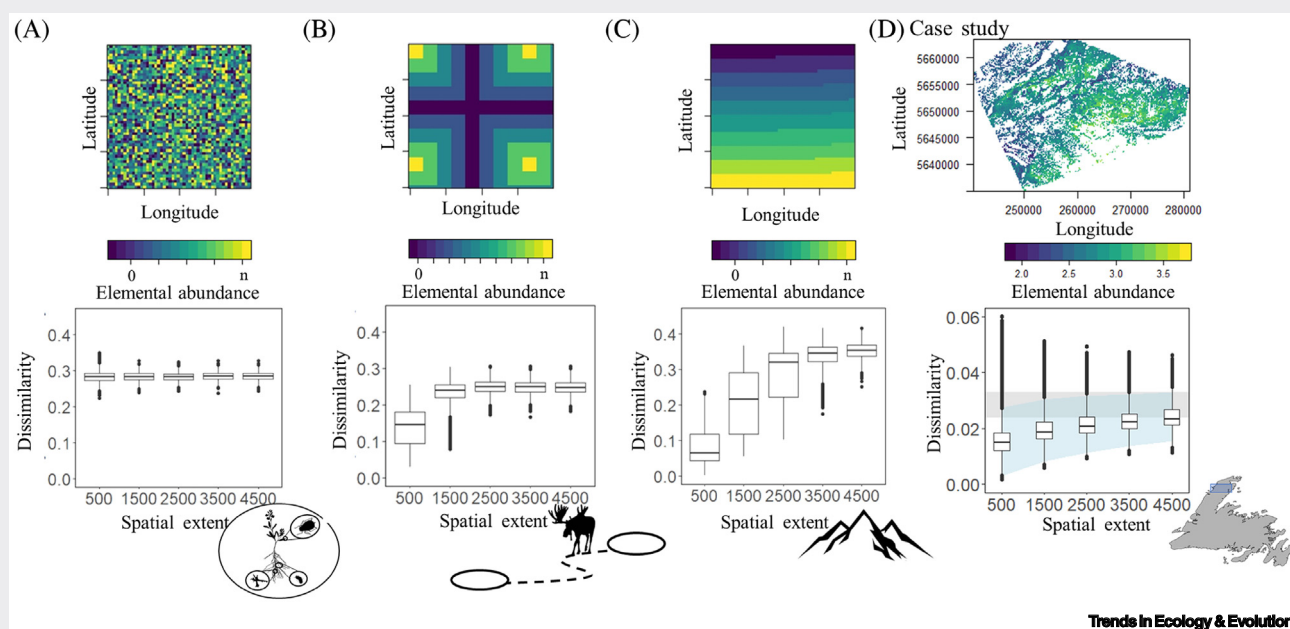
Figure I. Hypothetical data (A–C) and potential drivers for distributions of four different elements demonstrate how different elemental distributions result in characteristic relationships integrating information from each element using community ecology metrics. These scenarios can be compared with the distribution of nitrogen, phosphorus, calcium, and magnesium in real landscapes (D) [15], where a random null model is plotted in light gray, and light blue is the standard error (SE) from the stoichiometric distribution model (StDM) uncertainty (±1 SE for each StDM coefficient). Researchers could develop different null models to test different hypotheses and evidence in support of different drivers of elemental dissimilarity.

by the abiotic mixing of surface and ground waters at the aquatic–terrestrial boundary (Figure 2) [8], and by biotic drivers, such as terrestrial ungulates foraging on aquatic plants [40]. Indeed, by studying elemental distributions using traditional dissimilarity metrics alongside newer metrics, such as LCBDs, we can go beyond elemental maps to developing hypotheses about the abiotic and biotic processes that may be shaping elemental distributions (Figure 2). This approach also extends to consider community function, since elements are the building blocks of ecosystems.
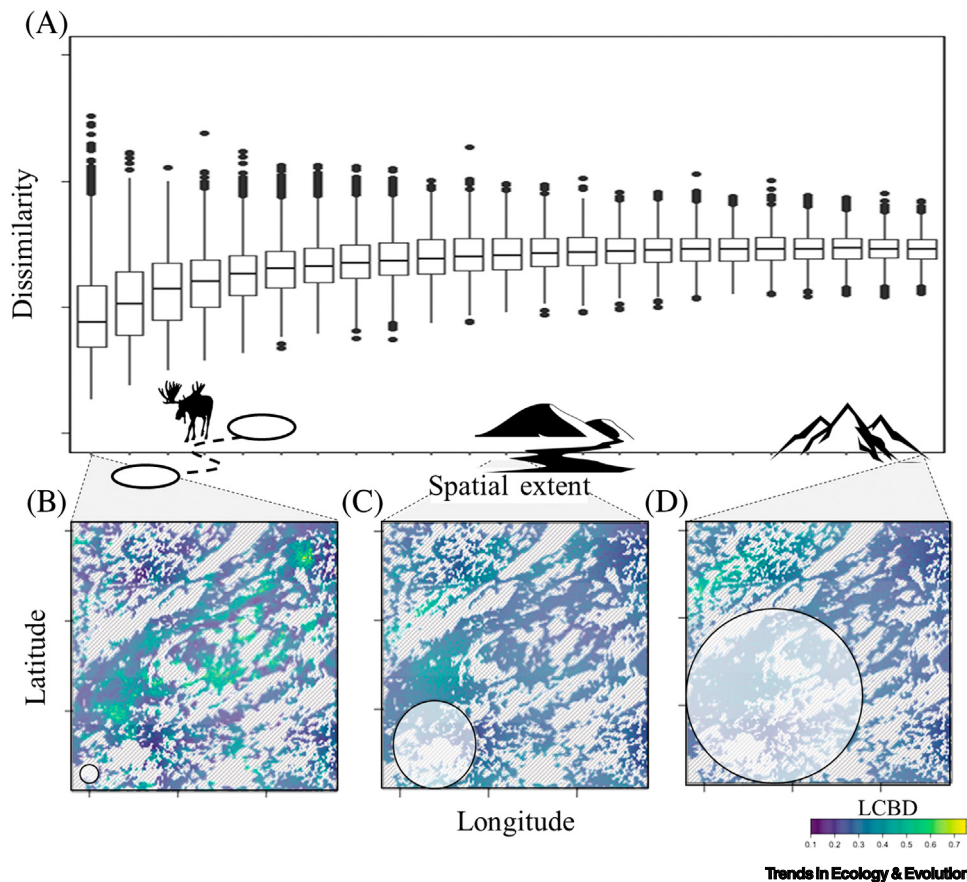
Figure 2. Identifying ecosystem control points across the landscape. The drivers of elemental diversity are expected to change as spatial extent increases. Approaches such as the local contribution to β-diversity (LCBD) help identify cells that contribute more or less to elemental diversity. In particular, this is useful for seeing how the contribution of an individual cell changes with increasing spatial extent. For example, at small extents ([e.g., size of circle on (B)], we see the emergence of patches that contribute more to elemental diversity [i.e., the green to yellow cells in the center of (B)]. This suggests that small-scale abiotic and biotic processes are responsible (e.g., preferential foraging or recycling). At larger extents [e.g., size of circle in (C)], we see less patchy distributions of cells across the landscape, yet they are more abundant closer to the aquatic–terrestrial boundary [aquatic areas on the plots are denoted by light-gray areas (C)]. Finally, as β-diversity reaches its landscape asymptote, we see a homogenous distribution of cells across the landscape (D). Cell resolution is 30 m, and spatial extent increases, with circles demonstrating the extent for the three insets (B–D). Data are from white birch (*Betula papyrifera*) foliage stoichiometry collected at sites in Newfoundland, Canada by Leroux *et al.* [15] and integrate nitrogen, phosphorus, calcium, and magnesium distributions.

From elemental diversity to community structure

Building expectations on what spatial patterns of elements should look like is critical because plants and animals not only affect, but also respond to the distribution and **stoichiometry** of elements. For example, plots containing tree species with calcium-rich detritus have a greater diversity and biomass of earthworms [41]. The increased biomass of earthworms then has the potential to support larger communities of consumer species, such as birds [42] and/or microbial species [43,44], a potential direct example of the link between resource element diversity and species diversity. This example gives a single element perspective; however, an increase in calcium concentration should be reflected in a higher LCBD for these plots compared with surrounding plots. Thus, we hypothesize that spatial heterogeneity in elements could relate to coexistence dynamics and community structure, directly influencing the number of available niches and biodiversity [45,46].

Biodiversity is one contributor to ecosystem function, while food web structure is another. Evidence suggests that element availability can alter food web structure in appreciable ways. For example, an aquatic mesocosm experiment from the Netherlands [47] demonstrated that the great pond snail (*Lymnaea stagnalis*), an aquatic omnivore, responded to changes in stoichiometry of *Potamogeton lucens*, a native plant. Specifically, with eutrophication, the plant carbon (C):nutrient ratio decreased, causing the omnivore to increase its reliance on plant resources [47]. Stronger interactions between omnivores and plants increase top-down control of the plant community with broad ramifications for food web stability [48,49]. Moreover, the stability of the system depends on which nutrient is limiting. For example, in a laboratory experiment, Larsen *et al.* demonstrated that, under P limitation, cyanobacteria are better able to resist pathogenic phages and, as a consequence, communities are more stable when there is P limitation as opposed to N limitation [50].

Plants, animals, and ecological networks do not exist in isolation; instead, they are connected across scales via flows of organisms and nutrients. Through biotic processes, such as mobile consumers, biota can respond to heterogeneity in nutrient abundance, driving nutrient flows across the landscape through recycling, altering consumer coexistence, and preferentially favoring a single ecosystem [51,52]. In particular, meta-ecosystem theory illustrates the intimate feedback between the biotic and abiotic components of ecosystems, and how patch-specific biotic (e.g., organismal dispersal) and abiotic (e.g., inorganic nutrient runoff) processes can affect community structure and ecosystem function [7,53,54].

We hypothesize that changes in elemental diversity should be reflected directly in the structure of biotic communities, a promising avenue to investigate that may provide a long-sought mechanistic link between community and ecosystem processes that can be measured directly in the field. Consequently, gathering empirical data to measure and quantify how spatial patterns in elements vary across spatial extents is critical to diagnose how ecosystems are being shaped by the current era of rapid change (Box 2).

Box 2. Harnessing empirical data

Human activities are significantly modifying both biotic [64] and abiotic [65] components of ecosystems, with implications for the distribution and flux of elements (see [66] for examples of how human activities have modified the movement of biota). Yet, our basic understanding of the causes and consequences of the spatial distribution of elements is limited, especially as we extend beyond just C, N, and P and embrace a diversity of elements [67]. Encouragingly, the number of studies on ecological stoichiometry has increased dramatically in recent years, demonstrating the perceived utility of elements for understanding key drivers of community structure and ecosystem dynamics (reviewed in [68]). As a result, there has been the development of databases of georeferenced elemental data for different taxa across the globe (e.g., [69]). Such databases may provide response variables in StDMs with predictor variables derived from remote-sensing products (e.g., MODIS [70]). Alternatively, other remotely sensed products (e.g., soilGrid [71]) may also contain spatially explicit predictions of elemental distribution and could be used to study elemental landscapes at much larger scales. One drawback of these data sets is that they typically only include C, N, and P; however, more recently, researchers have recognized the importance of considering additional elements, such as sodium (e.g., [72]), potassium (e.g., [73]), and magnesium (e.g., [74]). These data sets represent an excellent starting point for applying our proposed community ecology of elements across different ecosystems.

Further exploration of our proposed framework could link these elemental data sets with other ecological data sets such as animal movement data sets from Movebank (e.g., [66]) to see whether the landscape ecosystem control points of elemental diversity correlate with consumer movement patterns [75]. Alternatively, returning to the same landscapes and resampling over many years can help explore temporal patterns in elemental diversity. Again, by coupling these resources with biodiversity data, particularly data for organisms with quick generation times (e.g., microbial communities), the power of biota to change elemental abundance can be determined. For example, van Beest *et al.* [22] investigated geochemical landscapes in the high Arctic, demonstrating how they affect reproductive success of muskoxen (*Ovibos moschatus*), matching long-term muskoxen survey data with a sampling of 14 essential and nonessential elements in soil and vegetation. Extending the soil and vegetation sampling over a couple more seasons would be invaluable for teasing out further long-term impacts of **zoogeochemical** processes.

Beyond essential elements

Thus far, our perspective omits a suite of nonessential elements, which have a pivotal role in the functioning of ecosystems and focuses on elements rather than molecules, thus overlooking heterogeneities in availability and mobility of elements. Among nonessential elements, heavy metals, such as lead or mercury, can be toxic to most organisms, and are responsible for a range of population-level effects on wildlife, such as embryonic development in fish populations [55]. While these elements are naturally occurring, human activities can increase their concentration, such as in the case of mercury used in precious metal extraction and, thus, found in high concentrations near mines [56]. Considering molecules rather than elements also holds the potential to discern between substances of variable toxicity, bioavailability, and lability, which can, in turn, provoke ecosystem-wide modifications, such as eutrophication due to nitrate leaching [57]. Similar to essential elements [15], there has been progress in the development of spatial models for predicting and mapping the distributions of contaminants *sensu lato* across landscapes [58]. Our approach can be extended beyond essential elemental diversity to general chemical diversity, a critical step given that theory is beginning to recognize the importance of ecosystem processes on contaminant concentrations [59,60].

Concluding remarks

Biotic and abiotic processes affecting the distribution of elements are often interdependent. Researchers have already taken advantage of this interdependence through the stoichiometric niche, which provides a common currency in community description and reduces the number of axes required to characterize communities [61]. Here, we provide a framework that complements that approach by describing the elemental landscapes upon which these communities are built, a fundamental step if we are to disentangle the mechanisms behind the biotic and abiotic processes determining these community niches. In particular, it provides researchers with a coherent empirical framework to: (i) study and analyze empirical patterns of elemental distribution across spatial extents; and (ii) link **geodiversity** to the biotic components of ecosystems [32]. Our community perspective on elemental diversity has the potential to generate questions about, and insights into, important drivers of community structure and biodiversity (see Outstanding questions), but its applications do not stop there. Most conservation planning focuses on the protection and restoration of species, populations, or communities, despite a call toward 'ecosystem-based management' in terrestrial, freshwater, and marine biomes [62]. In many ways, a pivot toward considering ecosystem control points for conservation is akin to calls for considering species interactions [63], that is, levels of diversity beyond the species that may be critical to maintain ecosystem functioning. In this era of unprecedented global change, our work to link geodiversity with biodiversity provides a holistic perspective in the service of ecosystem management.

Declaration of interests

None declared by authors.

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Outstanding questions

How does elemental β-diversity scale with spatial grain across different ecosystems? Elemental data from individual forage plant species can be used to test the hypothesis that elemental β-diversity in resource elements follows predictable patterns with spatial scale.

How do relationships between elemental β-diversity and spatial grain change depending on the source material for elemental data? The choice of soil samples or plant tissues may reflect different abiotic or biotic processes (e.g., different plant species can extract elemental resources from different depths).

Is there a relationship between changes in elemental β-diversity and the structure of biotic communities? By coupling elemental data with telemetry data for consumer species, researchers can determine whether the spatial grain at which the change in elemental dissimilarity is the greatest is also the grain size at which organisms are most active in their foraging.

How do local contributions to elemental dissimilarity (i.e., ecosystem control points) relate to patterns of species diversity? Specifically, we hypothesize that high spatial turnover in elements should lead to more functional complementarity in communities flagged with high local contribution to elemental dissimilarity, and generally higher levels of ecosystem function.

If local ecosystem control points are strongly correlated with species diversity, as would be expected based on niche-partitioning opportunities, then elemental landscapes are important considerations for conservation efforts. Is the global protected areas network conserving ecosystem control points and if not, in which biomes are there key gaps?

Ecosystem control points may be important features to protect or restore. Can we use our elemental landscapes to identify limiting nutrients to help protect and restore function to some of our degraded landscapes? Alternatively, can we develop contaminant landscapes to identify areas of the landscape to focus remediation efforts?

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