DISPATCH

Biodiversity: The role of interaction diversity

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Links between the diversity of ecological interactions and community structure have long been recognised but remain broadly understudied. A new study concludes that vertebrate trophic interaction diversity is nearly uncorrelated with either phylogenetic or functional biodiversity and largely reproduces flora-defined bioregions.

Ecological communities comprise complex networks of organisms which interact with one another and their environments to produce the beautiful natural systems in which we all exist. Fundamentally, ecology aims to understand and conserve this complexity by mapping a set of generalisable metrics, rules and concepts. As with understanding any complex system, this requires simplification. As an analogy, a power grid can be measured in terms of its component parts; energy enters the grid via various generation mechanisms (wind, solar, hydroelectric, coal, etc.), which all have different measurable characteristics, and heterogenous spatial and temporal organisation. In ecology, there is increasing focus on the diversity of measurable traits (characteristics) and on the relatedness of organisms, rather than only counting species (Figure-1)[1-3]. However, not only the component parts must be measured and understood but also their interactions through space and time. Despite long-term recognition of the importance of interaction diversity, the role that interactions play in shaping biotic community dynamics and broader ecosystem functioning has been widely overlooked and is primarily situated within the realm of theoretical or experimental studies[4]. This lack of focus on interaction diversity is due, in part, to a lack of data on the richness and abundance of biotic interactions for most systems, particularly across large geographical areas [5], but this is now changing. In 2020, the 'Tetra-EU 1.0' dataset was published[6], a 'trophic metaweb' of potential pairwise interactions between European tetrapod species across trophic levels, extracted from the literature. In this issue of *Current Biology*, a new paper by Pierre Gaüzère, Wilfried Thuiller and colleagues[7] uses the Tetra-EU 1.0 dataset to map Europe-wide patterns of trophic interaction diversity and to compare that interaction diversity with functional and phylogenetic biodiversity. More accurately — given that all three of these aspects of biodiversity correlated strongly with species richness — they first calculated the residuals from the fit with species richness in each case, to produce 'corrected' measures. The residuals were then mapped and correlated with each other. This provides a better insight into how — alongside other diversity types (Figure 1) — the diversity of biotic interactions can help us to understand and conserve our complex natural world.

Two of the findings by Gaüzère and colleagues[7] are particularly interesting: first, after controlling for species richness, the trophic interaction diversity in 10-km grid squares across Europe is nearly uncorrelated with either functional or phylogenetic diversity. This indicates that interaction diversity adds considerable information on community structure, with likely implications for community functioning. Second, mapping the diversity of these trophic interactions between vertebrates produces regions that are quite similar to the existing biogeographic regions of Europe, which are largely based on the vegetation. This suggests that these bioregions capture fundamental aspects of ecology that span organismal groups.

Interaction diversity may provide insights in addition to those derived from other biodiversity components. For example, it is well understood that disturbances, such as fire, shift not only the taxonomic diversity of communities but also their functional and phylogenetic compositions[8]. Returning to the analogy of a power grid, greater interactions between power supply and demand will tend to be more resilient — a large, power-hungry factory connected to wind, solar and gas-generated electricity will be more resilient to reduction or loss in supply (e.g. no wind) than a factory with only a single supply link. Interaction diversity may therefore facilitate identification of ecological communities that are more resilient (high interaction diversity) to projected widespread species extinctions and compositional changes[7]. Realised resilience will depend on trophic community structure, species richness as well as the strength, richness and abundance of biotic interactions, as found in both theoretical[4] and empirical studies[9]. For instance, in longleaf pine ecosystems, higher interaction diversity in more frequently burned sites played an important role in ensuring regional ecosystem stability[5].

In parallel to potentially indicating ecosystem resilience, interaction diversity can indicate human impact on ecological communities, for instance as a signature of loss of interactions[1] or gain in network connectivity. After correcting all diversity components for relative species richness, Gaüzère and colleagues[7] found that there was little or no correlation between corrected trophic interaction diversity of European vertebrates and either corrected functional or corrected phylogenetic diversity. For example, although there is functional and phylogenetic similarity between communities in the Alps and Carpathian Mountain ranges, the loss of top predators due to human pressures in the Alps has led to a reduction in total relative trophic interaction diversity[7]. Therefore, although there are still limitations for the study of interaction diversity, particularly in terms of availability of high-quality interaction data (aka the Eltonian shortfall [10]), its study adds to the biodiversity conceptualisation toolbox for enhancing conservation understanding and decision making [1].

When incorporating interaction diversity into explanations for key ecological hypotheses, perhaps the most obvious benefit is its clear link to ecosystem functioning, such as pollination or nutrient cycling[5]. Interactions can be divided into three main types, based on their function within ecosystems: additive interactions affecting functioning between two functional units, keystone interactions impacting broader community-wide functioning and redundant interactions undertaken by multiple species within an ecosystem[9]. An example of a keystone interaction is seed dispersal of plant species by Neotropical primates, mainly via defaecation, providing additional nutrients for secondary seed dispersers or seed consumers[11].

At broad scales, additive, keystone and redundant interactions operate collectively to structure regional ecosystems. For example, Gaüzère and colleagues[7] found evidence for the role of interaction diversity in shaping community structure. Specifically, they found that regions defined by corrected trophic interaction diversity of vertebrates across Europe were largely coincident with existing bioregions. This is interesting because the bioregions (e.g. the Boreal biogeographic region) are defined by spatial organisation of vegetation[12], which was not included in their data. Diversity of trophic interactions could therefore be important in delineating structural differences between communities at the regional scale. In addition, the analysis of Gaüzère and colleagues[7] produced novel sub-regions with particular relevance to interaction diversity, such as the Mediterranean Basin. The exact implications of regional differences require further research, particularly into the turnover of interactions across spatial scales.

From the extensive literature on biotic interactions, we may expect interaction diversity to provide important and novel insights into a range of ecological hypotheses[10] (Figure 2). For example, high trophic interaction diversity (relative to species richness) in boreal communities compared with low functional and phylogenetic diversity could be attributed to broader trophic niches of boreal species[7]. Testing the generalisability of correlations between interaction diversity and latitudinal gradients in other diversity components could help elucidate the mechanisms that drive the latitudinal diversity gradient[13]. However, as with the study by Gaüzère and colleagues[7], the literature on the latitudinal gradient in biotic interactions has almost solely considered trophic interactions[13]. A key step in better using interaction diversity is to move beyond trophic, pairwise interactions to understand how different types of interactions operate collectively to affect ecosystem functioning[4,14]. For example, facilitation interactions, such as those provided by nurse plants — such as *Parkinsonia microphylla* providing shaded microhabitats for establishment of the cactus *Carnegiea gigantea* in the Sonoran desert — , might differ in importance between latitudes due to latitudinally varying environmental stress gradients, or as climate changes, and be modulated by complex multi-level interactions[15]. Facilitation might provide a key role in both structuring communities and determining future range-shifts under climatic changes at species range limits[16]. For instance, the general trend under climatic changes of higher drought-stress and lower cold-stress in lower-latitude alpine communities was found to lead to a decrease in cold-tolerant facilitators and an increase in drought-tolerant facilitators not seen in higher-latitude mesic environments[17]. The generality of these findings awaits further research. Studying both trophic and non-trophic biotic interactions will be assisted by increased data collection using novel techniques; for example, behavioural interaction diversity within and between species is increasingly being studied using biomimetic robots[18]. To maximise the usefulness of future data collection on biotic interactions for producing generalisable conclusions, care should be taken to standardise collection methods and the functional units between which interactions are recorded[10].

An important consideration for studying interaction diversity is its scale-dependence. Different interaction types, for different taxa, are likely to vary in importance for ecosystem functioning at different spatial resolutions, as found in a study on the interaction diversity of woodpecker and other bird species in the USA[19]. Therefore, studies on interaction diversity should always aim to use ecologically relevant spatial grains[5]. Further investigation is required to better understand how and why interactions differ between regions, for instance by correlating interactions to climatic variables to understand environmental drivers[20], or to variables such as biomass, to understand the links between interactions and ecosystem productivity. However, the ambitious scale of the study by Gaüzère and colleagues[7] provides a first glimpse at the additional insights that interaction diversity provides for understanding macroecological patterns.

Declaration of Interests

The authors declare no competing interests.

Figure 1. Five key types of biodiversity.

Five key types of diversity combining to build our conceptualization of overall biodiversity. Taxonomic, functional, and phylogenetic diversity are routinely mapped across regions or continents to understand the relative number, characteristics and eco-evolutionary relatedness of diversity units across space and through time. Conversely, metabolomic diversity (the relative diversity of chemical processes involving metabolites within biological organisms) and interaction diversity (diversity of biotic interactions) are underutilised but are subjects of increasing interest at synoptic scales.

Figure 2. Key insights from interaction diversity.

Examples of four key insights that interaction diversity can provide for ecology. Top left: Hotspots of interaction diversity may indicate higher resilience to future ecosystem perturbations (interaction diversity decreasing from theoretical habitat ‘a’ to habitat ‘d’). Top right: Relative decay of interaction diversity through time may indicate relative human pressures. Bottom left: Different interactions are expected to operate variably as spatial scale and extent change. Bottom right: Interactions link to key ecosystem functions.

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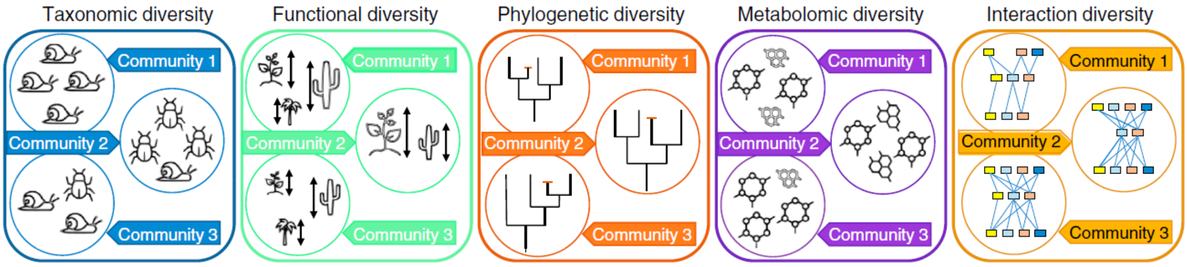
Figures:



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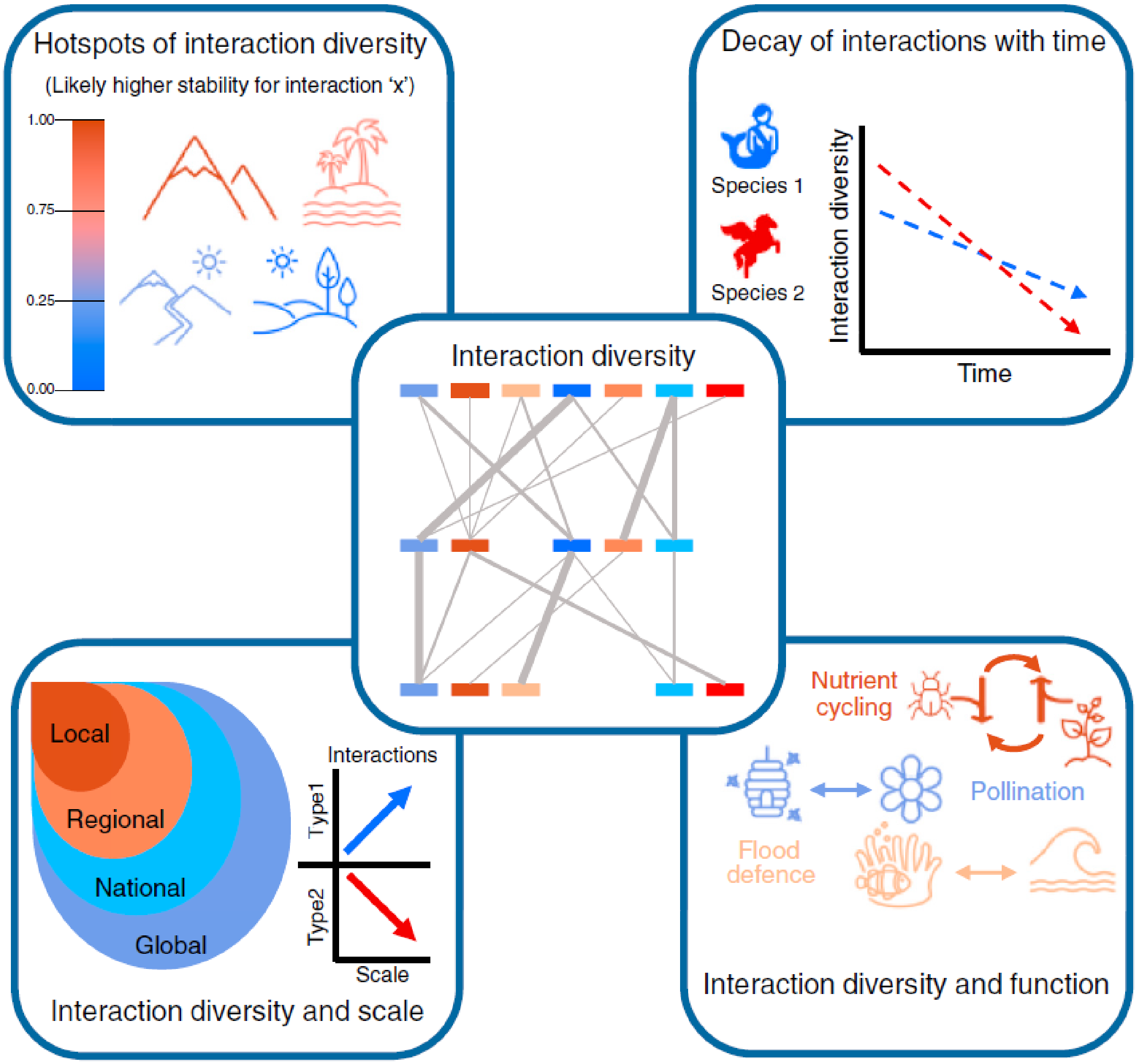

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