

## Forum

## Diversity–functioning relationships across hierarchies of biological organization

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Numerous biodiversity–ecosystem functioning (BEF) experiments have shown that plant community productivity typically increases with species diversity. In these studies, diversity is generally quantified using metrics of taxonomic, phylogenetic, or functional differences among community members. Research has also shown that the relationships between species diversity and functioning depends on the spatial scale considered, primarily because larger areas may contain different ecosystem types and span gradients in environmental conditions, which result in a turnover of the species set present locally. A fact that has received little attention, however, is that ecological systems are hierarchically structured, from genes to individuals to communities to entire landscapes, and that additional biological variation occurs at levels of organization above and below those typically considered in BEF research. Here, we present cases of diversity effects at different hierarchical levels of organization and compare these to the species-diversity effects traditionally studied. We argue that when this evidence is combined across levels, a general framework emerges that allows the transfer of insights and concepts between traditionally disparate disciplines. Such a framework presents an important step towards a better understanding of the functional importance of diversity in complex, real-world systems.

Keywords: biodiversity–ecosystem functioning (BEF), ecological hierarchy, emergent properties, genetic diversity, landscape diversity, levels of organization, scaling

## Introduction

Since the 1990s, an increasing number of biodiversity–ecosystem functioning (BEF) experiments have addressed the consequences of biodiversity for the productivity of synthetic plant communities (Hooper et al. 2005). The research discipline that evolved

from these studies broadened the perspective on biodiversity from it being a consequence of biogeographic and eco-evolutionary processes (Violle et al. 2014) to being a cause of ecosystem functioning. The general finding that emerged is that species-rich communities are, on average, more productive than species-poor communities (Hooper et al. 2005, Schmid et al. 2008, Cardinale et al. 2012, Weisser et al. 2017). Such biodiversity effects can emerge from the inter-specific partitioning of abiotic resources such as nutrients, light and water (McKane et al. 2002, von Felten et al. 2012, Williams et al. 2017), which leads to a more complete and more efficient community-level use of these resources. Further, there is evidence that interspecific facilitation, where the presence of a species improves the performance of another, increases productivity in mixed cultures (Wright et al. 2017), and that interactions with mutualists and escape from pathogens and consumers (partitioning of enemies) can also play a role (Schnitzer et al. 2011, Turnbull et al. 2016, Holt and Bonsall 2017, Huang et al. 2022). The specific biological processes that underpin biodiversity effects vary depending on species, ecosystem, and environmental context. Nevertheless,

the phenomenological pattern that emerges – a productivity increase in mixed compared to the average monospecific community – remains remarkably constant (O'Connor et al. 2017, Hong et al. 2022).

In BEF experiments, communities are typically systematically assembled from a species pool, with the same species occurring at low and high diversity. In the simplest case, a two-species community produces more biomass than the average of the two monocultures (*overyielding*; Schmid et al. 2008). Additive partitioning schemes have been developed to decompose overyielding into statistical selection and complementarity effects (Loreau and Hector 2001, Fox 2005, Isbell et al. 2018) based on the distribution of relative yields of species grown in mixed-species communities (Box 1). In the majority of multi-year BEF-experiments, overyielding is primarily related to statistical complementarity effects (Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012, Weisser et al. 2017, Wagg et al. 2022). Note that such *selection* and *complementarity effects* are phenological descriptions of response patterns, irrespective of the actual biological mechanisms that cause them. For example, complementarity

### Box 1. Patterns and mechanisms underpinning diversity effects.

#### *Selection-probability and complementarity effects*

Net diversity effects are often described in terms of patterns of contributions of the system's components [e.g. genes, populations of individuals (=species), ecosystems] to the overall effect. A selection probability effect indicates that the functioning of a mixture is largely determined by a single component (or a minority of components), often accompanied with a reduced functioning of the other mixture components. Conversely, complementarity effects describe a case where all (or a majority of) components improve each other's function in mixture. These definitions are broader than in traditional BEF research for reasons of applicability across hierarchical levels.

#### *Statistical partitioning schemes*

The additive partitioning method (Loreau and Hector 2001) is widely used in BEF experiments (Cardinale et al. 2007, Fargione et al. 2007, Cadotte 2017, Weisser et al. 2017) to statistically decompose net diversity effects into complementarity effects (CE) and selection effects (SE). It is based on relative yield (yield of a species in mixture divided by its yield in monoculture, accounting for planted proportions) deviations in mixture from those expected under the null model that individuals of species perform identically in mixture and in monoculture.

The additive partitioning requires the individual contributions of the parts in a system to its functioning to be separable. It is therefore unsuitable when functions can only be determined at the whole-system level, such as in the case of intra-individual genetic diversity.

#### *Biological processes*

Complementarity and selection probability effects (and similarly CE and SE from statistical partition schemes) are phenomenological descriptions of how net diversity effects result from the contributions of the system's components. Thus, they indicate mere 'effect patterns' rather than specific biological processes (Barry et al. 2019).

In a plant community, a complementarity effect may emerge from the partitioning of abiotic resources such as nitrogen (McKane et al. 2002, von Felten et al. 2012), reducing interspecific competition, and increasing community-level resource use. The same complementarity effect may equally result from the accumulation of species-specific consumers or pathogens at the higher host densities found in low-diversity communities, which will drive conspecific negative density dependence and associated benefits of growing in mixtures (Schnitzer et al. 2011). Species may also promote the productivity of other species by enhancing their environment (facilitation) (Wright et al. 2017). Fundamentally different biological mechanisms may thus give rise to the same net diversity effect phenomenon, even within a single level of the ecological hierarchy (here: plant communities).

effects can occur due to a wide range of mechanisms including resource partitioning, facilitation, and interactions with pathogens and mutualists.

A limitation of the additive partitioning scheme is that it requires the functioning value of a system to be split into additive contributions by its individual components. For community biomass, this evidently is possible because it equals the sum of the biomass of the component species. In other cases, which we will discuss here, this is no longer possible. For example, it is not possible to split the performance of an individual into additive genetic contributions of its parents. Therefore, we here use the terms *selection probability effect* and *complementarity effect* in a broader, more conceptual sense (Fig 1, Box 1). We use the term *selection probability effect* (sensu Aarssen 1997) to refer to the case in which the functioning of a system is predominantly driven by one (or few) of its components. Conversely, we use the term *complementarity effect* to refer to the case in which all (or many) of the components of a system contribute to its functioning.

## Diversity metrics

It is evident that the community-level benefits of species richness are related to functional differences among species (Loreau 2000). However, the decisive traits, and how they drive overyielding, remain largely elusive (van der Plas et al. 2020). Clearly, some species are functionally more similar than others, and the amount of diversity that effectively promotes community productivity is therefore sometimes better captured by functional

trait diversity measures (Mouchet et al. 2010, Lefcheck and Duffy 2015, Cadotte 2017), or, assuming that functional traits are to some degree evolutionary conserved, by phylogenetic diversity (Flynn et al. 2011). Finally, there are also metrics that measure diversity at a coarser (e.g. plant functional types Reich et al. 2004, Fry et al. 2014) or finer (e.g. genotypes; Crutsinger et al. 2006) resolution than species.

A fact that is not often noted is that these diversity metrics all quantify variation among classes of individuals in the community. In the case of species richness, individuals are first classified according to their species identities, i.e. into populations, and then the number of resulting classes is counted to obtain species richness. For plant functional-type richness, a similar but coarser classification of individuals is performed, using class demarcations that typically run along phylogenetic lineages (e.g. legumes, graminoids). Similarly, for genotype diversity, the classes define groups of individuals within species. Finally, for functional diversity metrics, classes are assigned average trait values, for example by species, and these values are then combined into a community-level metric of functional trait variation (Cadotte et al. 2011). Overall, traditional BEF research therefore focuses on inter-individual diversity, typically determined at the level of classes such as species, to explain emergent properties at the community and ecosystem level.

## Diversity effects generalized

The complexity found in ecological systems is often described as a hierarchy of structures in which each level is composed

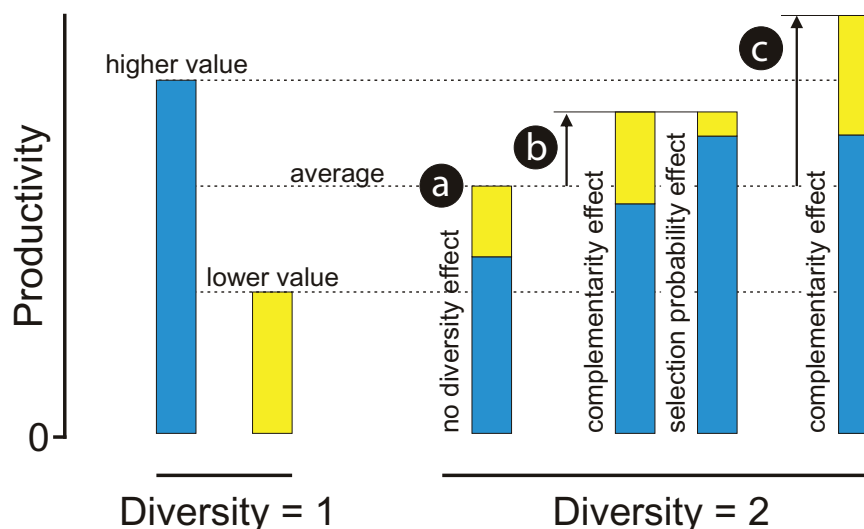


Figure 1. Diversity effects, overyielding, and selection probability and complementarity effects. In this example, communities are either composed of a single species (left, diversity of one) or of two species (right, diversity of two). The blue species has a higher monoculture productivity than the yellow species. The null expectation is that the yield of the mixture equals the average yield of the monocultures (A) when both species are initially established at half their monoculture density. The mixed community is said to overyield when its productivity exceeds the expected average value (B, C). The special case of transgressive overyielding occurs when mixture productivity exceeds the productivity of the most productive monoculture (C). Overyielding may occur because both species benefit from growing in mixture (complementarity effect), or because one species dominates mixture productivity, with unchanged or even reduced productivity in the other species (selection probability effect). Note that here we refer to complementarity and selection probability effects conceptually, not in the sense of the additive partitioning scheme (Box 1).

of basic units from lower levels (Fig. 2). For example, a landscape may be described using the lower levels ecosystems, communities, populations, individuals, genes, etc. Crucially, interactions between units at one level can lead to emergent functions at higher organizational levels (Korn 2005). In the traditional BEF framework, the interacting units are classes of individuals, typically species, that interact and thereby affect community productivity (Fig. 2b–c).

Given this ecological hierarchy, an important question is whether positive diversity–functioning relationships also occur at levels of organization other than the species (or alternative classes of individuals) that constitute communities (Box 2). In other words, we ask whether other entities also interact so that functioning at higher levels of organization is improved when the units combined are more diverse. For example, could a landscape composed of different ecosystem types (forests, grasslands, etc.) have higher landscape-level productivity than a landscape with a single ecosystem type? Or could positive diversity–functioning relationships also occur within individuals? If this is the case, can these effects be described using the same concepts as in community ecology? And, finally, could a generalized framework be developed to describe diversity effects across multiple levels of organization? In the following, we present evidence for BEF-type diversity effects at hierarchical levels below (within individuals) and above (across landscapes) those typically

considered in BEF research. We then discuss commonalities, differences, and research questions that arise on the way to a framework of diversity effects across hierarchies.

### Diversity at the sub-individual level

In traditional BEF studies, classes of individuals (typically species) are the basic units that interact to affect community and ecosystem functioning (Fig. 2b–c). Focusing on individuals themselves as the system (Fig. 2d; Reeve and Keller 1999), diversity can be identified at the levels of traits, functions and genes. As in BEF experiments, where species composition is manipulated and typically consists of mixtures and monocultures of the component species, here we are primarily concerned with systems in which corresponding low-diversity systems exist, and in which it is plausible that effects occur due to diversity per se.

Plant leaf traits vary within an individual (Schmid and Bazzaz 1994, Hulshof and Swenson 2010, Blonder et al. 2013). One example are leaf angles and orientation that vary considerably within a canopy; plagiotroph and erectotroph leaves tend to dominate in the lower and upper part of the canopy, respectively, but there also is variation within a single canopy layer. Leaf angles are affected by environmental context (light), and reference plants exposed to the same light environment but having only plagiotroph or only erectotroph leaves

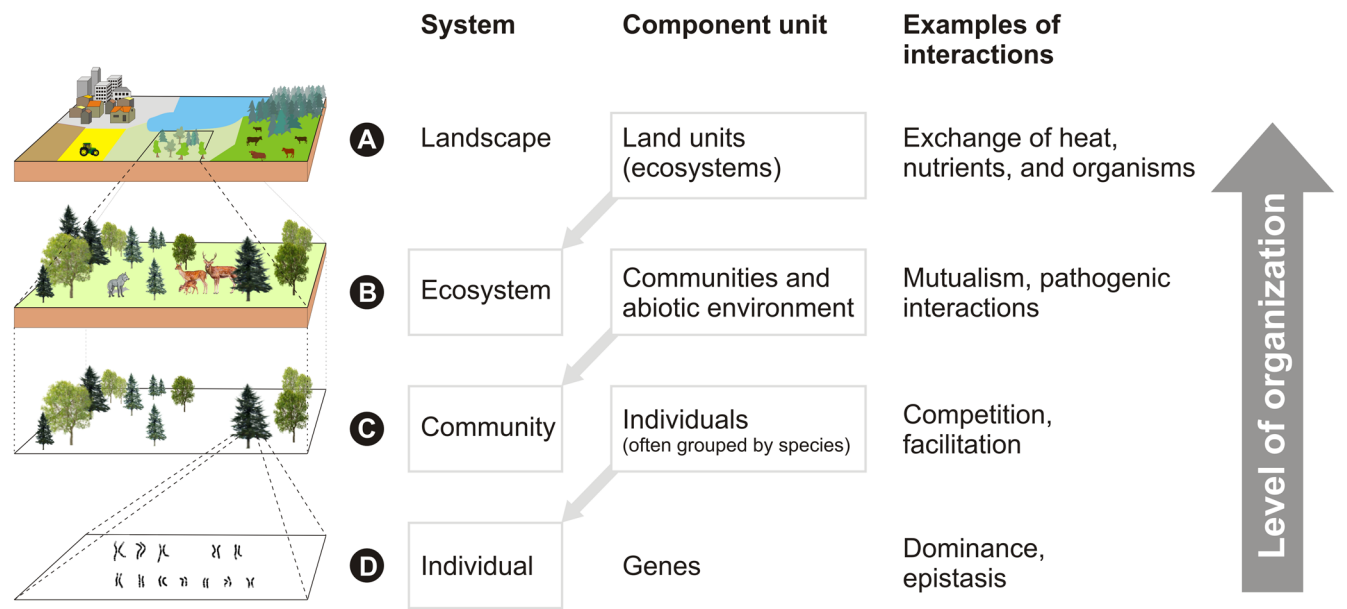


Figure 2. Complex ecological system as hierarchy of nested units. Here, we focus on four levels: landscapes containing ecosystems; ecosystems containing communities plus their abiotic environment; communities containing individuals; and individuals containing genes. In BEF research, a plant community is understood as a system of interacting units which are classes of individuals such as plant functional types, populations (all individuals of a species within the system), or genotypes (C). The emergent effects of the diversity of these units are then observed at the level of the community (C) or ecosystem (B). Moving down the hierarchy, individuals may be considered systems that are composed of units such as genes (D). Conversely, moving up the hierarchy, ecosystems may be considered basic units that form larger systems, namely landscapes (A). At each hierarchical level, the specific mechanisms underpinning the interactions among component units differ; nevertheless, diversity effects phenomenologically similar to the ones found at the community and ecosystem level (B, C) may also emerge at other levels of the hierarchy. For example, genetic diversity within individuals may affect functioning at the level of individuals (D), and ecosystem-type diversity may affect the functioning of entire landscapes (A).

## Box 2. Scaling diversity–functioning relationships.

### *Spatial scaling*

Landscapes contain species, communities, and ecosystems that form a spatial mosaic of patches. The resulting networks of patches are referred to as meta-populations, meta-communities and meta-ecosystems. The flows of organisms, genes, and matter within and between these networks can modify local species richness and ecosystem functioning (Hanski 1998, Mouquet and Loreau 2003, Krauss et al. 2010, Fahrig et al. 2011, Gounand et al. 2018). An active area within BEF research therefore is concerned with scaling BEF relationships from the local ecosystem scale to such spatial networks (Isbell et al. 2018, Gonzalez et al. 2020, Qiu and Cardinale 2020, Wang et al. 2021). While such scaling accounts for spatial structures at a level higher than the ecosystem, the basic units of diversity used to explain functioning remain the same (typically species).

### *Hierarchical scaling*

Diversity exists at levels of organization other than inter-individual diversity within ecological communities (e.g. species diversity), such as genetic diversity within individuals and diversity of ecosystem types within landscapes. A perspective fundamentally different from traditional BEF research is to consider entities at these other levels (e.g. entire ecosystems) as fundamental units that determine the diversity at a higher organizational levels (e.g. a landscape). At each level of organization, specific emergent types of diversity effects occur, many of which are not captured by established scaling approaches. Integrating diversity–functioning relationships across hierarchical levels therefore requires novel conceptual frameworks.

### *Spatial selection effects*

Studies of BEF effects in heterogeneous landscapes have revealed landscape-scale patterns that underpin system-level functioning. For example, the productivity of diverse plant communities might, at the local scale, be dominated by a few species (a selection effect [SE], Box 1). These SE might be driven by different species in different communities found in a larger landscape, reflecting different environmental conditions. The landscape-level pattern that emerges corresponds to a complementarity, i.e. there is a spatial division of labor among different locally dominant species (and the communities in which they exist). In a recently proposed spatial and temporal extension of the additive partitioning, this phenomenon is described as spatial selection effect (Isbell et al. 2018, Loreau et al. 2021).

Interestingly, patterns comparable with spatial selection effects also occur at the sub-individual level. Specifically, genetic diversity within individuals promotes individual-level functioning, a phenomenon known as heterozygosity, or, when parents are more distantly related, heterosis. The sets of alleles contributed by the parents can be seen as elements of diversity (richness of 1 for inbred offspring, otherwise 2). A dominant effect of a superior over a deleterious allele at a single locus can be seen as selection probability effect. A spatial selection-type effect occurs when dominant alleles from different parents are suppressing deleterious alleles at different loci in the hybrid, i.e. when the parents have complementary distribution of superior alleles among loci.

do not exist. It therefore becomes very difficult to experimentally show that leaf angle variation per se is advantageous, but this can be done mathematically using light interception models (Plekhanova et al. 2021).

Another form of intra-individual diversity is cell differentiation. A simple example are heterocysts in cyanobacteria. Many cyanobacteria are capable of fixing  $N_2$  using the nitrogenase enzyme, which is  $O_2$ -sensitive and therefore in conflict with photosynthesis, which produces  $O_2$ . Heterocyst cyanobacteria solve this problem by separating out  $N_2$  fixation into specialized thick-walled cells (the heterocysts) that provide an anaerobic environment. Non-heterocyst  $N_2$  fixing cyanobacteria also exist, but many of these are only able to fix  $N_2$  under anaerobic or micro-aerobic conditions, or in the dark when no photosynthetic activity takes place (Stal 2012, Berrendero et al. 2016). The nitrogenase of cyanobacteria can also be protected from  $O_2$  in other ways (Bergman et al. 1997), but overall it seems safe to conclude that the evolution

of specialized, functionally complementary cell types can provide diversity benefits to organisms. Similar benefits likely also exist in more complex cases such as tissue differentiation in different organs, but this is more difficult to show because of a lack of less-diverse reference systems.

At the genetic level, genomes, genes and alleles within individuals may be considered the basic units of intra-individual diversity (Fig. 2d). An important functional manifestation of within-individual genetic diversity in plants is heterosis, which occurs when hybrids perform better than the average of the two parents (Birchler et al. 2010). In the following, we consider examples in diploids and polyploids and draw parallels to species-level BEF studies, focusing on overyielding and the underlying selection probability and complementarity effects. Diploids possess one allele from each parent and hence, the offspring of genetically dissimilar inbred parents have a higher intra-individual allelic diversity than offspring obtained by selfing the parents. This genetic diversity often results in trait

values (e.g. biomass, stress tolerance) above the mean of the parental values (mid-parent heterosis; [Birchler et al. 2010](#)), or even higher than the best parent (better-parent, or high-parent heterosis; [Plech et al. 2014](#)). This conceptually corresponds to overyielding and transgressive overyielding in BEF research ([Fig. 1](#)). The exact mechanisms of heterosis are debated ([Birchler et al. 2010](#)) but an important aspect is that in hybrid offspring, recessive deleterious alleles are complemented with superior alleles from the other parent. When functioning is determined by the superior allele only (dominance), BEF researchers would describe this as a selection probability effect. The analog of complementarity effects appears when positive interactions occur among parental alleles at a single locus (overdominance), when multiple deleterious alleles are distributed among different loci in the two parents (complementary distribution of superior alleles), or when positive non-allelic interactions among different genes (epistasis) promote a trait ([Birchler et al. 2010](#), [Jiang et al. 2017](#), [Fujimoto et al. 2018](#)). In BEF experiments, transgressive overyielding is strong evidence of complementarity effects ([Tilman et al. 1997](#), [Loreau 2004](#)); similarly, high-parent heterosis indicates genetic interactions beyond simple single-locus selection probability effects. In BEF experiments, overyielding tends to increase with functional trait distances among individuals ([Cadotte 2017](#), [Wagg et al. 2017](#)), and similarly heterosis generally becomes larger with genetically more dissimilar parents ([Birchler et al. 2010](#), [Pandey et al. 2018](#), [Wei and Zhang 2018](#)). However, genetic incompatibilities can also lead to outbreeding depression and hybrid inferiority ([Plötner et al. 2017](#)), especially when genetic differences are large ([Moll et al. 1965](#), [Nosil et al. 2005](#)).

In autopolyploids, plants hold more than two homolog chromosomes and therefore may carry more than two alleles at a locus. When comparing autopolyploids with a given ploidy level, e.g. tetraploids, heterosis typically increases progressively with allelic diversity ([Levings et al. 1967](#), [Groose et al. 1989](#), [Riddle and Birchler 2008](#)). The incremental heterotic gains decrease as allelic diversity increases, comparable to BEF experiments in which the largest gains per extra species occurs at low diversity ([Reich et al. 2012](#), [O'Connor et al. 2017](#)). In both cases, this decelerating increase in system-level function is compatible with the idea of a higher functional redundancy in more diverse systems, at least when considering one function within a time and space ([Hector and Bagchi 2007](#), [Isbell et al. 2011](#)).

Allopolyploids combine subgenomes of typically diploid ancestor species and are an interesting case because the combination of divergent genomes results in a form of fixed heterozygosity. Studies of allopolyploids of wild wheat *Aegilops* ([Huynh et al. 2020](#)) have shown that their environmental niches resemble the combined niches of their diploid progenitors. In other words, the combination of complementary (divergent) suites of genes (subgenomes) within an organism enables allopolyploids to more fully exploit resources in a temporally or spatially heterogeneous environment (a larger 'biotope space'; [Dimitrakopoulos and Schmid 2004](#)), similar to how different species can form a larger total community niche ([Salles et al. 2009](#)) when growing in mixture.

Such effects have also been documented in studies of bittercress (*Cardamine*) species along local soil moisture gradients ([Akiyama et al. 2020](#)). Specifically, the allopolyploid *C. flexuosa* had a wider hydrological niche than its diploid ancestors *C. hirsuta* and *C. amara* that were restricted to the relatively dry and wet ends of the same gradient, respectively. Transcriptomic analyses suggested that *C. flexuosa* united the different stress responses (to drought and water logging) of its diploid ancestors, and that the resulting transcriptomic plasticity underpinned its wider environmental niche and allowed for a physically broader habitat.

## Diversity at the super-individual level

Moving up in hierarchy from traditional BEF experiments, one may consider ecosystems as new fundamental units that compose a larger landscape ([Fig. 2A](#)). In practice, these basic units may be defined as ecologically homogeneous and contiguous areas of land that are clearly delineated from each other. Such *land units* ([Zonneveld 1989](#)), corresponding to individuals in community ecology, could be classified into land-unit types like forests, lakes, agricultural lands, or urban areas, corresponding to species. The set of land-unit types present defines the diversity and composition of a landscape ([Tscharnke et al. 2012](#)).

As with the other hierarchical levels, we ask whether interactions among dissimilar land-unit types, whatever their nature, add up to systematically higher functioning at the landscape level. Empirical studies directly addressing this topic are only beginning to emerge. An example is a study by [Oehri et al. \(2020\)](#) in which the remotely-sensed productivity of 6–25 ha landscapes increased with land-unit type richness. In analogy to BEF experiments, this study built on a pool of land-unit types that occurred in equal proportions at all levels of diversity, i.e. land-unit type abundance remained statistically unconfounded with land unit diversity.

What mechanisms may drive such land-unit type diversity effects? First, landscapes with a higher land-unit type diversity may harbor more different species within particular land-unit types, which in turn might affect the productivity of individual land units through the well-documented positive effects of local ( $\alpha$ ) species diversity ([Cardinale et al. 2011](#), [O'Connor et al. 2017](#)). For example, discontinuities and environmental gradients at land-unit interfaces could create niche space that harbors other species than the more homogeneous interior of land units ([Stein et al. 2014](#), [Tukiainen et al. 2019](#)). This may explain why ecosystems often are more productive at their periphery than in their interior, as reported in forests ([Morreale et al. 2021](#)) or agriculture ([Bevis and Barrett 2020](#)). The spatial arrangement of land units may also promote emergent metapopulation ([Hanski 1998](#), [Hanski et al. 2017](#)) and metacommunity ([Mouquet and Loreau 2003](#), [Fahrig et al. 2011](#)) processes and thereby support a higher local species richness ([Shmida and Wilson 1985](#), [Hatton and Carpenter 1986](#); Box 2, 'Spatial scaling'). In agricultural landscapes, pollinators and natural enemies residing in neighboring land units are of practical importance ([Fahrig et al. 2011](#), [Martin et al. 2019](#), [González-Chaves et al. 2020](#),

Massaloux et al. 2020), and diverse landscapes also hinder long-range pathogen transmission (Real and Biek 2007, Jones et al. 2011).

A second group of mechanisms may operate independently of species diversity (Box 2, 'Hierarchical scaling'). For example, Oehri et al. (2020) found that landscape diversity effects were related to the  $\alpha$ -diversity of land-unit types, and the latter was uncorrelated with local plant species richness determined in vegetation relevés. The biophysical mechanisms that underpin such emergent diversity effects are understudied to date, but there is evidence that land units interact in ways that could support such effects. For example, landscapes composed of a mixture of forest and grassland were found to be cooler than the average of homogenous landscapes ('monocultures') of either land-unit type (Mendes and Prevedello 2020). This climatic effect was likely driven by surface energy-balance differences among land-unit types, which, when forming a spatial mosaic (Leuzinger et al. 2015), destabilize atmospheric boundary layers and result in additional turbulence, convection, and advection (Hong et al. 1995) that redistribute matter (e.g. water) and energy (e.g. heat) within and among land units (Segal et al. 1988, Weaver and Avissar 2001, Tscharrntke et al. 2012, Gounand et al. 2018). Another idea is that land unit types contribute differently to the creation and spread of wildfires (Hoffmann et al. 2012, Marchal et al. 2017, Cano-Crespo et al. 2022), for example because they contain less fuel or high levels of humidity. It further has been observed that the size of islands in an archipelago correlates positively with fire frequency (Wardle et al. 1997) – simply because the probability to be hit by lightning scales proportionally to size, and because the island is the unit consumed by the fire. This patch-size effect may well also apply to mainland land units ('mainland islands') that contain particularly ignitable material, such as grassy savannah. Together, it thus may well be that a landscape more diverse in land-unit types is more resistant to 'consumption' by fire, and this consumption temporally more stable under climate extremes such as drought (Bond and Keeley 2005).

An intriguing aspect of such interactions among land units is that they can even involve surfaces largely devoid of above-ground plant cover, such as natural or artificial bare ground, water bodies, and to some extent, urban areas. These land units become increasingly important in human-dominated 'real-world' landscapes (Elhacham et al. 2020) but are rarely considered in observational biodiversity–functioning studies because the abundance of the plants that determine species diversity is often low. Temperate forest edges often are more productive than their interior (Laurance et al. 1997); for example a study found an increase of 36 and 24% in forest growth and biomass, respectively, when the adjacent land cover type was anthropogenic (Morreale et al. 2021). These land-unit interactions may involve the exchange of carbon, nutrients, water, and pollutants (Schmidt et al. 2017, Abbott et al. 2018). Enhanced nitrogen deposition at forest edges, for example, led to a 95% higher amount of carbon in aboveground biomass compared to 100 m interior in European deciduous forest edges (Meeussen et al. 2021). Other positive effects of diverse land units may be

attributes of the structure itself rather than just edge effects. For example, a study reported greater net N mineralization,  $N_2O$  fluxes, and gross rates of nitrification in small patches compared to large forest fragments within a landscape of interstitial grasses (Billings and Gaydess 2008). The authors controlled for edge and microclimatic effects by measuring the N-related fluxes from the patches in the laboratory rather than the field. The increased N cycling was attributed to larger quantities of root biomass in the small patch soil profiles in this grassland – forest ecotone. Similar productivity-enhancing interactions also have frequently been observed at terrestrial-aquatic interfaces (McClain et al. 2003, Ballinger and Lake 2006, Capon et al. 2013, Garner et al. 2015). All these types of interactions can affect functions, such as the productivity of particular land units, both positively (von Hardenberg et al. 2001, Bultman et al. 2014, Gounand et al. 2017) and negatively (Hanski 2015, Chang et al. 2021, Kabano et al. 2022). In plant communities, net positive interactions have been shown to outweigh the much less frequent negative ones (Wang et al. 2019, van der Plas 2019, Turner et al. 2020), but corresponding evidence for land-unit interactions is anecdotal so far (Oehri et al. 2020) and awaits systematic investigation. An interesting possibility, however, is that simple averaging effects are beneficial. For example, the circulation of heat and moisture in landscapes with a high diversity of land-unit types might stabilize local environmental conditions by a landscape-wide averaging. This buffering of climate extremes may in turn promote and stabilize landscape-wide productivity. Such effects are already leveraged in urban and landscape planning where green space and water bodies help reduce high temperatures in urban heat islands (Gunawardena et al. 2017, Qiu et al. 2017).

## Community-ecological concepts generalized

The processes that cause diversity effects clearly vary between (but also within) hierarchical levels of organization (e.g. interspecific nutrient partitioning, epistasis, landscape-wide heat and nutrient re-distribution). Interestingly, however, they result in comparable *phenomenological* patterns. It may thus be useful to analyze these patterns with similar approaches. In the following, we consider three domains: traits and functional complementarity, diversity metrics and multifunctionality, and the contributions of diversity at different hierarchical levels to system-wide functioning. We derive open research questions central to developing a general framework of diversity effects across hierarchies.

Can the concepts of functional complementarity and niches, as applied to species, be extended to other hierarchical levels? The environmental conditions under which a species is able to persist defines its fundamental niche, i.e. the set of environmental conditions that are suitable for the existence of a population of a species, without any other limiting factors present which could constrain the population (Hutchinson 1957). One may equally ask under which conditions a specific allele manifests as beneficial phenotype, or a particular land unit benefits from a certain climate or landscape environment. In community ecology, the niches of species often

remain theoretical concepts because their dimensions are difficult to quantify in practice (Kraft et al. 2015). However, the functional complementarity of species is sometimes approximated indirectly from differences in traits associated with the function in question (Wagg et al. 2017). Functional traits have also been attributed to entities such as land units (He et al. 2019, Valbuena et al. 2020, Lausch et al. 2020); such traits include spectral properties of the land surface, or the typical canopy height of vegetation types. We propose that such traits may characterize the functional differences among land units and thus serve as predictors of diversity effects. For example, functional differences between land-unit types that are mediated by surface energy-balance differences and consequent boundary layer instabilities could hence be characterized using land unit-type traits such as albedo or the fraction of absorbed energy that can be dissipated as latent heat by evapotranspiration (Burakowski et al. 2018).

Functional traits could further be expressed as *reactions norms*, i.e. as change in a phenotypic trait of a genotype or species along an environmental gradient (Wuest et al. 2021). This approach could be extended from genotypes and species to other organizational levels. In the example of the allopolyploid bittercress *Cardamine flexuosa* (Akiyama et al. 2020), the homoeolog genes in the two subgenomes are differently expressed along gradients of water availability, and these reaction norms indicate a functional subgenome complementarity that manifests as diversity effect (a broader niche) at the individual and species level.

Overall, functional trait-based diversity metrics (trait distances: Petchey and Gaston 2002, convex trait hulls: Cornwell et al. 2006, Mouchet et al. 2010, diversity measures obtained directly by remote sensing: Schneider et al. 2017) could serve as a surrogate of functional complementarity and help predict diversity effects that emerge at different levels of hierarchical organization. Such concepts may be even more easily applied at levels different from species and communities because their relevance for the processes that underpin diversity effects may be more evident, for example because they rest on well-understood physical processes (e.g. convection). This contrasts the species level where many different trait combinations often effectively represent 'neutral spaces' (Hubbell 2006) and thus do not support functional complementarity, and it also is difficult to distinguish relevant from functionally irrelevant and correlated traits.

The most fundamental metrics of diversity (e.g. richness) account just for the mere presence of distinct units in a system. However, the relative abundance of the components of a system may also matter. Experimentally, species abundance is more difficult to maintain in plant communities than species richness, but there is some experimental evidence that a high evenness of species abundances sometimes has beneficial effects similar to the ones of higher richness (Wilsey and Potvin 2000, Kirwan et al. 2007, Sonkoly et al. 2019). Similarly, some studies with polyploids show allelic dosage effects (Yao et al. 2013). For example, tetraploid hybrids derived from two inbred parental lines often show higher heterosis when the ratio of the parental genome is more even (e.g. higher vigour in 2:2 than in 3:1 hybrids; Groose et al. 1989).

Comparable evenness effects likely also exist at the super-individual level; for example, a landscape largely dominated by grassland with only a very small patch of forest may functionally approximate a grassland-only landscape. Describing and analyzing such effects of abundance across different levels of biological organisation will greatly be facilitated by a common mathematical framework. One such possibility was proposed by Gaggiotti et al. (2018), who argued that, first, many commonly-used diversity metrics (e.g. richness, functional diversity, phylogenetic diversity) can be modified to reflect abundances based on Shannon's entropy, and, second, that Shannon-diversity, although this is not commonly done, is applicable at the level of genetic diversity (frequency of alleles). They further highlight that these diversity metrics can be decomposed into components of within ( $\alpha$ ) and between ( $\beta$ ) system diversity. Nevertheless, it should be noted that richness is a more fundamental aspect of diversity than abundance, because the presence of species in itself implies the possibility of changes in abundance, for example when environmental conditions change. The presence of low-abundance species thus can lead to higher-order diversity-related phenomena such as spatial insurance effects (Loreau et al. 2003).

So far, we focused on a single ecosystem function (productivity), but diversity also drives multifunctionality, i.e. the ability to simultaneously provide multiple functions (Hector and Bagchi 2007, Manning et al. 2018, Gounand et al. 2020). This can occur if different species provide different functions (Isbell et al. 2011) and means that a diverse community is able to provide high multifunctionality (at least if intermediate levels of functioning are desired), even if there is no underlying complementarity among species for individual functions (van der Plas et al. 2016). Such processes could also occur at other hierarchical levels. Different land unit types provide different functions across a landscape, and particular combinations of land-unit types may strengthen different ecosystem services differently (Foley et al. 2005, Raudsepp-Hearne et al. 2010). For example, a herbaceous community may best support pollination services for agriculture, whereas forests may provide the best buffering of water flows in the landscape, or the best resistance against wildfire spread. Similarly, at the intra-individual level, different sets of genes support different functions (e.g. growth, drought resistance, or disease resistance), and different parental crosses will differently affect heterotic benefits in different traits. We therefore think that just as species diversity can be even more important for multifunctionality than for individual functions (Meyer et al. 2018), diversity effects at other organizational levels likely become stronger the more functions are considered.

Diversity effects at different hierarchical levels might also interact with each other. For example, genetic diversity within individuals (a lower level of organization) may interact with species diversity (a higher level or organization), similar to genetic diversity within a population interacting with species diversity to affect biomass production (Fridley and Grime 2010, Crawford and Rudgers 2012, Tang et al. 2022). High diversity at one hierarchical level could also functionally compensate for low diversity at another: genetic diversity in a dominant species has been shown to have similar effects on

functioning as species richness does (Cook-Patton et al. 2011, Crawford and Rudgers 2012) or coexistence (Lankau and Strauss 2007). High within-individual diversity in a dominant species, e.g. complementarity between subgenomes in an allopolyploid, might therefore compensate for low species richness, or vice versa. Alternatively, high diversity at multiple levels might be needed for high system-level functioning.

A related question concerns how diversity is best allocated across hierarchical levels to maximize the functioning at the uppermost hierarchical level of the system considered. While a certain diversity may be beneficial at any one level, negative effects may dominate past a certain threshold. For example, there are costs associated with at least some kinds of plasticity (DeWitt et al. 1998) and it may therefore be better to diversify functions across species rather than within an extremely generalist individual. Indeed, short-term evolutionary processes can lead to increased variation in species monocultures (van Moorsel et al. 2018) but increased niche separation between species in mixed-species communities (Zuppinge-Dingley et al. 2014). Similarly, realized niche breadth and the individual densities of rare species may become very small in an extremely species-diverse community, and multiple different ecosystem types (land-unit types) with each a lower  $\alpha$ -species richness but additional benefits of diversity effects among land-unit types may therefore result in a higher landscape-level functioning.

## Concluding remarks

By elaborating on phenomenologically similar effects of diversity at multiple levels of the ecological hierarchy, we emphasized an overarching commonality, namely that systems composed of a diverse set of units – on average – tend to function better than more uniformly-composed systems. Recognizing this general pattern may set the seed for a framework that integrates diversity effects across levels. A challenge on this path is that diversity-related phenomena at different levels are investigated by disparate science disciplines and in part described using terminology that does not focus on diversity.

There is an increasing need to scale traditional BEF studies to complex systems such as real-world landscapes (Isbell et al. 2017, Oehri et al. 2020, Gonzalez et al. 2020). In these, diversity effects will simultaneously operate at multiple hierarchical levels, and effects emerging from diversity components other than local species richness – the factor manipulated in traditional BEF experiments – will need to be considered. To date, some of these are largely uncharted terrain (e.g. effects at the landscape level), although there is evidence for their functional importance. Addressing these challenges will require a close collaboration across disciplines, including community ecologists, population geneticists, landscape ecologists and earth observation scientists.

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## Author contributions

**Sarah Mayor:** Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Eric Allan:** Writing – review and editing (equal). **Florian Altermatt:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Forest Isbell:** Writing – review and editing (equal). **Michael E. Schaepman:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Bernhard Schmid:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Pascal A. Niklaus:** Conceptualization (equal); Funding acquisition (equal); Writing – original draft-Lead, Writing – review and editing (equal).

## Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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